INTRODUCTION

Iguanidae*[1] is a large family (*ca.* 54 genera and 546 species) of lizards found in the Americas, the Fiji Island group and the Tongatapu and Va'vau groups in the Tonga Islands in the southwest Pacific Ocean, and Madagascar and the Comoro Archipelago in the western Indian Ocean (Fig. 1). The unusual distribution of the family may be an artifact of paraphyly; to date, no apomorphies have been presented to support the monophyly of Iguanidae* exclusive of the Australo-Afro-Asian Acrodonta (Agamidae* [35 genera, 319 species; Wermuth, 1967; Moody, 1980] + Chamaeleonidae[2] [6 genera, 128 species; Klaver and Böhme, 1986]) (Fig. 1). Indeed, Schwenk (1988) has suggested that one group of iguanids (anoles) may be more closely related to Agamidae* + Chamaeleonidae than to other iguanids. Both Agamidae* and Chamaeleonidae have been recognized universally by modern systematists, although monophyly of Agamidae* remains ambiguous (*contra* Moody, 1980; Borsuk-Białynicka and Moody, 1984).

Iguania (Iguanidae* + [Agamidae* + Chamaeleonidae]) has been established as the sister-taxon of Scleroglossa (=Scincogekkonomorpha [Sukhanov, 1961]), the non-iguanian members of Squamata (i.e., other lizards and snakes) (Camp, 1923; Estes *et al.*, 1988; but see Northcutt, 1978) and, as such, can be assumed to be of great antiquity. Even though the earliest fossil iguanid is from the Upper Cretaceous (Estes and Price, 1973), fossil acrodonts (e.g., †*Mimeosaurus**) are also known from the Upper Cretaceous, and several scleroglossan squamate groups were well-diversified by the Upper Jurassic (Estes, 1983a,b). Thus, if the hypotheses of squamate phylogeny are correct, Iguania must have been present in the Jurassic.

Major, likely monophyletic, groups within Iguanidae* were first recognized by Etheridge (1959, 1964, 1966, 1967), Etheridge *in* Paull *et al.* (1976), and Etheridge and de Queiroz (1988). As currently understood, Iguanidae* is composed of eight monophyletic groups of uncertain relationships to each other or to Agamidae* + Chamaeleonidae. These groups are: (1) anoloids (11 genera; >200 species); (2) basiliscines (3 genera; 9 species); (3) crotaphytines (2 genera; 7 species); (4) iguanines (8 genera; 25 species); (5) morunasaurs (3 genera; 11 species); (6) oplurines (2 genera; 7 species); (7) sceloporines (10 genera; 105 species); and (8) tropidurines (14 genera; 182 species).

The purpose of this study is to reevaluate the evidence for relationships within Iguania as well as to investigate the possible paraphyly of Iguanidae* with respect to Agamidae* + Chamaeleonidae, and Agamidae* with respect to Chamaeleonidae, and to provide a taxonomy logically consistent (Hull, 1964; Wiley, 1981a) with the recovered phylogeny within Iguania.

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[1] We use an asterisk beside a taxonomic name (the metataxon convention—Gauthier, 1986; Gauthier *et al.*, 1988 [cf. Donoghue, 1985]) to denote a nominal supraspecific taxon for which evidence of either monophyly or paraphyly is ambiguous or absent. Although this practice cannot be applied to unitary lineages (=species) (Frost and Hillis, 1990; but see Donoghue, 1985, and de Queiroz and Donoghue, 1988) we "flag" some monotypic fossil genera in this way to denote the lack of character evidence for grouping specimens under these binomials. Although, as used here, the metataxon convention is substantively the same as the shutter quotation convention of Wiley (1979), in this paper quotations surround names that represent nominal taxa that are demonstrably not monophyletic, but whose correction is outside of the scope of this paper. Because the historical reality of metataxa is questionable, their treatment as entities rather than sets in text is arbitrary. Casual collectives (e.g., agamids) are not asterisked because they are not formal names and as such are treated as are other casual collectives (e.g., lizards).

[2] Because this family-group name is based on the Latin *Chamaeleo*, rather than the Greek *Chamaeleon*, the formation of the family-group name must be Chamaeleonidae, rather than the oft-used Chamaeleontidae.

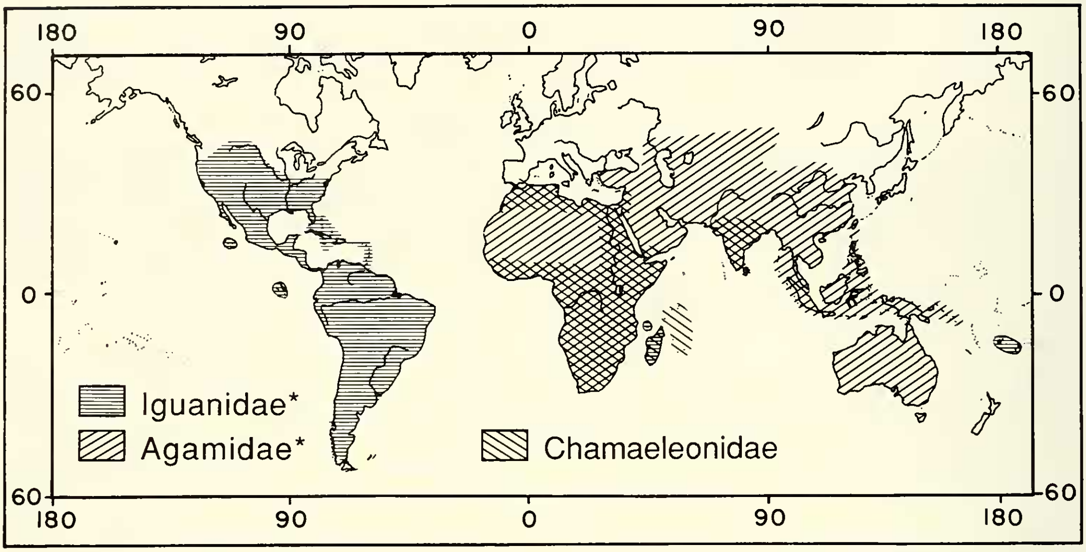

Fig. 1. Distribution of Iguanidae*, Agamidae*, and Chamaeleonidae.

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METHODS

The principles guiding this study are those of phylogenetic systematics (Hennig, 1966; Eldredge and Cracraft, 1980; Wiley, 1981b). Out-group comparison has been selected as the most general means of deciding on the polarity of character transformation series (Stevens, 1980; Watrous and Wheeler, 1981; Arnold, 1981; Farris, 1982; Maddison *et al.*, 1984; Kluge, 1985; Brooks and Wiley, 1985; de Queiroz, 1985). Following the evidence of Camp (1923), Gauthier *et al.* (1988), and Estes *et al.* (1988), Scleroglossa (=Scincogekkonomorpha = all non-iguanian squamates) was selected as the first taxonomic out-group, and Rhynchocephalia (including †*Gephyrosaurus* Evans, 1980, 1981) was selected as the second taxonomic out-group. These taxa were used to determine, where possible, the polarity of particular transformation series.

Using information from the literature (e.g., Moody, 1980; Borsuk-Białynicka and Moody, 1984; Arnold, 1984; de Queiroz, 1987; Etheridge and de Queiroz, 1988; Estes *et al.*, 1988; Lang, 1989), checked and augmented by our observations (see "Acknowledgments" for reference to collections in which specimens were examined), we constructed a character matrix of 67 transformation series for the operational taxonomic units selected (see next section). A few traditionally used characters were excluded from this analysis, either because they were autapomorphies of the taxonomic units, or because the characters within the transformation series suffered from insurmountable characterization problems, i.e., they could not be evaluated with any success across all taxonomic units. The data matrix was subjected to analysis using PAUP (Phylogenetic Analysis Using Parsimony) version 2.4.1 (Swofford, 1985) and, late in the development of the manuscript, Hennig86 version 1.5 (Farris, 1988). Within PAUP the data matrix was analyzed using the multiple parsimony (MULPARS) and global swapping (SWAP = GLOBAL) procedures. Global swapping allows the program to search for more parsimonious trees by global (as opposed to "nearest neighbor") swapping of branches. MULPARS allows the swapping procedure to be performed on all topologically distinct trees of a given length, rather than the first tree found of any particular length. Although character optimization followed the method of Farris (1970) (the default in PAUP), use of the BLRANGE (that calculates maximum and minimum branch links) and CSPOSS (that notes character ambiguity on all but terminal stems) options, as well as comparison with the DELTRAN option (that prefers convergence to reversal) output, and evaluation of the distribution of "unknown" character assignments allowed characters of ambiguous placement to be detected. Within Hennig86, the branch-breaking (bb) heuristic approach was employed. Tree optimization was evaluated using the consistency index (C.I.) of Kluge and Farris (1969). Results from multiple runs of both PAUP and Hennig86 were evaluated, and alternative rootings (i.e., placement of the hypothetical "ancestor") checked using MacClade version 2.1 (Maddison and Maddison, 1987).

We did not regard characters of variable placement to constitute particular evidence of relationship. That is not to say that we regard the various character optimization procedures as equally "likely"; in this case, we were merely trying to find evidence of relationship that did not require additional assumptions about how character evolution proceeds.

Some transformation series were used that could not be polarized by appeal to out-groups. In these cases, the "ancestor" cells in the data matrix were coded as unknown ("9" in PAUP; "?" in Hennig86). These unpolarized transformations were polarized within the analytical programs by correlation with the most parsimonious trees generated by the independently polarized transformations. Because the polarity of a transformation affects only rooting of the overall network rather than efficiency of the network, inclusion of these kinds of transformations is required if we are trying to find the most parsimonious explanation for all of the data.

Additionally, in some multiple-step transformations, additivity of the steps was not maintained because of lack of evidence of order of transformation; these transformations were treated as if any transformation between characters was one step ("unordered"). In some instances of these "unordered" transformations, the ancestral condition could be deduced even though the polarity of transformations beyond this initial condition could not be; in this case the "ancestor" was coded, but the transformation was treated as unordered. This allowed setting the initial condition of the transformation(s) without affecting subsequent transformations within the unordered set.

In some instances, a character could not be evaluated for a particular species. Or, in some cases where we used deduced ancestors as taxonomic units, the ancestral character was not deducible. In these cases, the character was coded as "unknown" for those taxa. The analytical programs allow for this contingency by making "what if" assignments minimally in disagreement with the otherwise most parsimonious arrangement of the characters on the tree.

We have not employed differential character weighting. This practice has been argued against by Patterson (1982) and Novacek (1986). Thus, the analysis was allowed to proceed as though the probability of undetected homoplasy was distributed equally across all transformation series. However, should the assumption that the plasticity of transformation series was historically equal prove to be wrong, or our *a priori* assessments of homology prove to be wrong, our results will have to be reevaluated.

CHOICE OF TERMINAL TAXA

A phylogenetic analysis is only as rigorous as is allowed by: (1) the historical reality (=monophyly) of the terminal taxa; (2) the quality of characterization of the transformation series; (3) the accuracy of *a priori* assessment of homology and relative historical plasticity of character transformation; and (4) the appropriateness of the out-groups employed. Our out-group structure, although difficult to use because of widespread homoplasy and relative apomorphy, is as good as current understanding of phylogeny within Lepidosauria allows (Gauthier *et al.*, 1988; Estes *et al.*, 1988). Although some characterization problems remain in several of the transformation series, these have been minimized as much as possible. With regard to terminal taxa, we could use the largest monophyletic groups that we had confidence were substantially corroborated. Traditionally, in a taxon as large as Iguania, this would mean we might employ genera as our operational taxonomic units. However, a number of these nominal genera are paraphyletic, and using these with their derivative taxa could cause unforeseen problems in data analysis. Our solution was to use the largest monophyletic generic and suprageneric groups for which "ancestral" characters could be deduced adequately. To minimize the number of "unknowns" ("9" in PAUP; "?" in Hennig86) in the data matrix, we would subdivide terminal taxa as far as necessary. However, in some cases these "ancestral" characters could not be deduced and the character assignment was "unknown." The terminal taxa that we employed were:

A. Acrodonts.—(1) †*Priscagama**; (2) agamas (agamids, excluding *Uromastyx, Leiolepis,* and *Physignathus*); (3) *Uromastyx*; (4) *Leiolepis*; (5) *Physignathus*; (6) chameleons. Acrodonta has its monophyly supported by a number of unique features, including maxillaries in broad contact behind the premaxilla (Moody, 1980; Estes *et al.*, 1988). A number of other features support the monophyly of the group, if it is assumed that the first functional out-group of this taxon is Iguanidae*. Traditionally, within Acrodonta, Agamidae* and Chamaeleonidae have been recognized, with Uromastycidae being recently resurrected, but subsequently provisionally synonymized with Agamidae* (see discussion in Borsuk-Białynicka and Moody, 1984).

Although Uromastycidae has been considered monophyletic (Moody, 1980, 1983a), the genera within this group, *Uromastyx* and *Leiolepis*, differ from each other in so many features that we have treated them as separate taxonomic units. *Physignathus*, although hypothesized as the sister-taxon of the remaining agamids (Moody, 1980 [unweighted analysis]), is also more easily treated separately. For purposes of deducing ancestral characters for agamas we provisionally accepted the phylogeny of Moody (1980).

The monophyly of chameleons is supported by so many features, such as zygodactyl feet, extremely extensile tongue, failure of the pterygoid to meet the quadrate (Rieppel, 1981), and reduction of the number of cervical ribs, that their monophyly has never been questioned. Hillenius (1986) and Rieppel (1981, 1987) considered *Brookesia* to be the sister-taxon of the remaining chameleons, but Klaver and Böhme (1986) considered *Brookesia* + *Rhampholeon* to be the sister-taxon of the remaining chameleons. We have not entered this discussion and have accepted only polarity decisions congruent with both views.

Additionally, we have included the extinct taxon, †*Priscagama** (Borsuk-Białynicka and Moody, 1984) in the hopes that inclusion of this putative agamid would allow a more clear resolution of acrodont phylogeny. At least one feature, the presence of both the anterior and posterior mylohyoid foramina in the splenial, may support the monophyly of †Priscagaminae* of Borsuk-Białynicka and Moody (1984), including, at least, †*Priscagama** and †*Mimeosaurus**. However, it might be argued that the anterior mylohyoid foramen is joined with Meckel's groove in Recent acrodonts (a further apomorphic condition that renders the monophyly of †Priscagaminae* arguable). Additionally, the pleurodont dentition of †*Pleurodontagama** Borsuk-Białynicka and Moody (1984) argues for paraphyly of †Priscagaminae*.

B. Anoloids.—(7) *Polychrus*; (8) *Enyalius*; (9) "*Pristidactylus*"; (10) para-anoles; (11) anoles. The monophyly of the anoloids is corroborated *a priori* by the character endolymphatic sacs extending into the nuchal musculature (Etheridge, 1959; Etheridge and Williams, 1985; Etheridge and de Queiroz, 1988); this feature is found otherwise in some chameleons within Iguania, and geckoes within Scleroglossa.

Polychrus is united by a large number of characteristics (e.g., third and fourth toes of equal length), but no hypotheses of phylogeny of the species have been proposed. Etheridge and de Queiroz (1988) regarded *Polychrus* as the sister-taxon of the other anoloids, but this arrangement is regarded as provisional.

Enyalius, "*Pristidactylus*," *Diplolaemus*, and *Leiosaurus* (including *Aperopristis*) form a group, the leiosaurs, that has its monophyly corroborated by the possession of subdigital scales divided distally (Etheridge and Williams, 1985; Etheridge and de Queiroz, 1988). *Enyalius* is the likely sister-taxon of "*Pristidactylus*" and its derivative taxa (*Diplolaemus* and *Leiosaurus*) (Etheridge and de Queiroz, 1988). Following the phylogenetic arrangement as posited by Etheridge and de Queiroz (1988), ancestral characters for "*Pristidactylus*" are coextensive with the characters of the non-*Enyalius* group of leiosaurs, and can be deduced from the Chilean group of "*Pristidactylus*" (*alvaroi*, *valeriae*, and *torquatus*) and the first two in-groups from this: "*P.*" *casuhatiensis*, and "*P.*" *achalensis*. *Enyalius* was treated as a distinct terminal taxon in order to avoid some deduced "unknowns" and because of its provisional association with the other leiosaurs.

The para-anoles (*Urostrophus** and *Anisolepis* [including *Aptycholaemus*, *fide* Etheridge and Williams, unpubl.]) may not form a monophyletic group (although Etheridge and de Queiroz, 1988, presented some evidence to support this conclusion); however, our analysis cannot distinguish between them. They have been treated together as the para-anoles.

The anoles (*Chamaeolis*,[3] *Chamaelinorops*, *Anolis*, and *Phenacosaurus*) clearly form a monophyletic group; this is corroborated by the greatly elongated second ceratobranchials, and having a distal pad raised under phalanges 2 and 3. *Chamaeolis* is likely the sister-taxon of the remaining anoles because it retains a free angular bone and palatine teeth (Etheridge, 1959). However, unlike Guyer and Savage (1986), we regard the phylogenetic structure within the remainder of the anoles to be problematic (Cannatella and de Queiroz, 1989).

C. Morunasaurs.—(12) "*Enyalioides*." Etheridge and de Queiroz (1988) have documented convincingly the monophyly of the morunasaurs ("*Enyalioides*," "*Morunasaurus*," and *Hoplocercus*), but have shown also that "*Enyalioides*" is paraphyletic with respect to "*Morunasaurus*,"

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[3] Usually unjustifiably emended to *Chamaeleolis*.

which, in turn, is paraphyletic with respect to *Hoplocercus*. "*Enyalioides*" *laticeps* is the sister-taxon of "*E.*" *praestabilis* + the remaining morunasaurs (Etheridge and de Queiroz, 1988). Therefore, the evaluation of ancestral characters within the morunasaur group is based on commonalities of these two species. The *a priori* assumption of monophyly of the morunasaurs is supported by the possession of enlarged nasal scales (Etheridge, 1969b) and greatly reduced vomers.

D. Basiliscines.—(13) *Basiliscus*; (14) *Corytophanes*; (15) *Laemanctus*. This phenotypically compact group is supported by one apomorphy, the posteriorly extended crest of the parietal (Etheridge and de Queiroz, 1988; Lang, 1989). Although other similar crests can be found in some anoles, some iguanines, and chameleons, the ontogeny of this crest makes it likely that these are nonhomologous (Lang, 1989). Because of the limitations of our deductive methodology we have considered the three monophyletic genera of basiliscines (Lang, 1989) to be terminal taxa, although it is reasonably clear that *Corytophanes* and *Laemanctus* form the sister-taxon of *Basiliscus* (Etheridge and de Queiroz, 1988; Lang, 1989). *Corytophanes* has three species, *Laemanctus* has only two; and *Basiliscus* has four in the relationship *B. vittatus* + (*B. basiliscus* + *B. plumifrons*) + *B. galeritus* (Lang, 1989).

E. Sceloporines.—(16) *Petrosaurus*; (17) *Sceloporus* (including *Sator*); (18) *Urosaurus*; (19) *Uta*; (20) *Phrynosoma*; (21) sand lizards (*Uma*, *Callisaurus*, and *Holbrookia*). The sceloporines have their monophyly supported by the sink-trap nasal apparatus (Stebbins, 1948), which involves an elongated septomaxilla. Additionally, they have unique hemipenes (Frost, 1987). Although the cladogram of Presch (1969) was supported by Etheridge and de Queiroz (1988), it is clear that the rooting of the tree is dependent on certain assumptions of out-group comparison that we do not want to make in this analysis. Therefore, for analytical reasons, we treat *Petrosaurus*, *Sceloporus*, *Urosaurus*, *Uta*, *Phrynosoma*, and the sand lizards as our terminal taxa, each of which is demonstrably monophyletic (Etheridge and de Queiroz, 1988).

F. Tropidurines.—(22) *Phymaturus*; (23) *Ctenoblepharys*;[4] (24) *Liolaemus*; (25) *Leiocephalus*; (26) "*Stenocercus*" + *Proctotretus*; (27) "*Tropidurus*"; (28) *Uranoscodon*. The tropidurines can not be supported as monophyletic *a priori* by any features relative to all other iguanians (Etheridge and de Queiroz, 1988), although they are phenotypically similar. Within the traditional tropidurines, however, a number of monophyletic groups can be discerned.

The *Liolaemus* group (*Phymaturus*, *Ctenoblepharys*, and *Liolaemus*) is supported by the possession of preanal pores, and although lacking in a few species, a recent analysis (Etheridge, unpubl.) indicates that this absence is due to loss. Etheridge and de Queiroz (1988) regarded *Phymaturus* as the sister-taxon of all others, the latter group now with more than 100 species. Although the majority of these are, and always have been, allocated to the genus *Liolaemus*, in recent years species have been variously assigned or transferred to the new and revived genera and subgenera *Abas*, *Ceiolaemus*, *Ctenoblepharys*, *Eulaemus*, *Ortholaemus*, *Pelusaurus*, *Phrynosaura*, *Rhytidodeira*, *Velosaura*, and *Vilcunia* (Cei, 1979a,b; Cei and Scolaro, 1982; Donoso-Barros, 1972, 1973; Laurent, 1983a,b, 1984, 1985; Nuñez and Yañez, 1983). Recent studies by Etheridge (unpubl.) confirm Laurent's (1984) decision to consider *Ctenoblepharys* as monotypic (*C. adspersus*), and the decision of Etheridge and de Queiroz (1988) to regard *Ctenoblepharys* as the sister-taxon of the remaining species. Although the remaining species form a monophyletic group, relationships within this group are not yet resolved, and in particular, there appears to be no support for the continued recognition of *Vilcunia*. Therefore, we include all species (i.e., we synonymize all of the generic names) not in *Phymaturus* or *Ctenoblepharys* within *Liolaemus*, which, so constituted, is monophyletic. Because of character-assignment problems, *Phymaturus* and *Ctenoblepharys* have been considered separately from *Liolaemus*.

Leiocephalus is monophyletic (Etheridge, 1966; Etheridge and de Queiroz, 1988; Pregill,

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[4] Usually unjustifiably emended to *Ctenoblepharis*.

unpubl.); this is corroborated by unique character distributions (e.g., parietal shelf shape and anterior process of the interclavicle), and the unique xiphisternal bars underlying the last sternal ribs[5] (Etheridge, 1967).

The "*Stenocercus*" group ("*Stenocercus*," "*Ophryoessoides*," and *Proctotretus*) is supported by one unique feature, extensive transverse hemipenial musculature (Arnold, 1984). Because "*Stenocercus*" is paraphyletic with respect to "*Ophryoessoides*" (which may be polyphyletic) (Frost, 1987), large-scaled "*Stenocercus*" and *Proctotretus* were used to determine ancestral conditions; the fine-scaled species of "*Stenocercus*" form a monophyletic group derived from this assemblage (Frost, 1987).

The "*Tropidurus*" group (*Uranoscodon*, "*Tropidurus*," *Tapinurus*, *Plica*, *Strobilurus*, and *Uracentron*) has its monophyly well corroborated by a number of apomorphies, none descriptively unique (e.g., enlarged interparietal scale, enlarged sternum), but not allowing paraphyly with respect to any other group. For analytical reasons, *Uranoscodon* (the sister-taxon of the remaining "*Tropidurus*" group [Frost, 1987]) is treated singly. Because "*Tropidurus*" west of the Andes is the sister-taxon of "*Tropidurus*" east of the Andes + *Tapinurus*, *Plica*, *Strobilurus*, and *Uracentron* (Frost, 1987; Böhme, 1988), "*Tropidurus*" was used to deduce the ancestral characters for the "*Tropidurus*" group, excluding *Uranoscodon*.

G. Crotaphytines.—(29) *Crotaphytus*; (30) *Gambelia*. The monophyly of the crotaphytines is not supported by any descriptively unique features, although they share a combination of features that, compared with any other iguanian group, suggests their monophyly. Because of this lack of *a priori* support of monophyly, we have treated *Gambelia* and *Crotaphytus* as terminal taxa.

H. Oplurines.—(31) *Oplurus*; (32) *Chalarodon*. The oplurines likely form a monophyletic group, corroborated by the possession of postxiphisternal inscriptional ribs forming paired splints (Etheridge, 1965; Etheridge and de Queiroz, 1988), and a black interparietal spot (Etheridge, 1969a). Although it is reasonably clear that *Chalarodon* and *Oplurus* are sister-taxa (but see *caveat* in Etheridge and de Queiroz, 1988) we treat them separately because deducing characters for the common ancestor of these taxa was unclear for several transformation series.

I. Iguanines.—(33) *Dipsosaurus*; (34) *Brachylophus*; (35) iguanas (other iguanines). The monophyly of the iguanines, the large, herbivorous iguanids, seems unassailable. Although shared with *Uromastyx* and *Hydrosaurus* in Agamidae* (Iverson, 1980, 1982), the presence of colic septa are likely a synapomorphy of this group, as is the position of the parietal process of the supratemporal (de Queiroz, 1987; Etheridge and de Queiroz, 1988). De Queiroz (1987) and Etheridge and de Queiroz (1988) argued that phylogenetically the iguanines have a basal trichotomy with: (1) *Dipsosaurus*; (2) *Brachylophus*; and (3) the remaining iguanines ([*Amblyrhynchus* + *Conolophus*] + *Ctenosaura* + *Sauromalus* + [*Cyclura* + *Iguana*]). These are the three taxa that we have accepted as terminal for purposes of our analysis.

TRANSFORMATION SERIES

Sources of the various transformation series are given. Apomorphies of Iguania and *a priori* autapomorphies of operational taxonomic units were excluded from this analysis; monophyly is assumed (see "Choice of Terminal Taxa"). The coding "0" denotes the plesiomorphic, and "1" (or higher) the hypothesized apomorphic character, unless the transformation series has been stated to be unpolarized or unordered, in which case the integer assignment is arbitrary. A character assignment of "unknown" refers to the condition being unobservable or of ambiguous assignment in that taxon. Character assignments for the out-groups are shown in Appendix 1 (character matrix).

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[5] The apparently similar xiphisternal bars in *Tapinurus* are associated with the myocommata of the *m. pectoralis major*, which is not the case in *Leiocephalus*.

1. **Premaxilla-nasal relationship** (Etheridge, 1966; Etheridge and de Queiroz, 1988).—(0) premaxillary spine overlaps nasal bones; (1) nasal bones overlap premaxillary spine. Because of interspecific variability *Phymaturus* is coded as "unknown."

2. **Maxillae** (Cope, 1864; Estes *et al.*, 1988).—(0) do not meet, separated by premaxilla; (1) meet broadly anteromedially behind palatal portion of premaxilla.

3. **Maxilla, posterior extent** (Moody, 1980; Borsuk-Białynicka and Moody, 1984).—(0) anterior to level of frontoparietal suture; (1) at, or posterior to, level of frontoparietal suture. Our observations indicate that *Crotaphytus* has the plesiomorphic condition (*contra* Borsuk-Białynicka and Moody, 1984). Chameleons are coded as "unknown" because *Brookesia* and some *Chamaeleo* have condition "0."

4. **Vomers** (Borsuk-Białynicka and Moody, 1984).—(0) flat or convex; (1) ventrally concave.

5. **Lacrimal** (Etheridge and de Queiroz, 1988).—(0) present; (1) absent. Chameleons are coded as "unknown" because of interspecific variability (Rieppel, 1981).

6. **Lacrimal foramen** (Etheridge and de Queiroz, 1988).—(0) lacrimal foramen not much larger than maxillopalatine foramen; (1) lacrimal foramen very much larger than maxillopalatine foramen.

7. **Skull rugosity** (Etheridge and de Queiroz, 1988).—(0) absent or restricted to frontal bone; (1) extensive and matching outline of overlying scales, found on other dermal skull bones besides frontal bone and matching outline of overlying scales. Although some *Sceloporus* (e.g., *S. poinsetti*) have this condition, it is unlikely to be the ancestral condition in that taxon. *Leiocephalus* is coded as "unknown" because of interspecific variation.

8. **Jugal, squamosal contact** (Moody, 1980; Lang, 1989).—(0) not, or barely in contact with squamosal; (1) broadly juxtaposed against squamosal along a transverse suture. Chameleons are coded as "unknown" because of interspecific variability (Rieppel, 1981).

9. **Postfrontal** (Estes *et al.*, 1988; Etheridge and de Queiroz, 1988).—(0) present; (1) extremely small or absent. *Phymaturus* is coded as "unknown" because of interspecific variability.

10. **Parietal roof shape** (Etheridge and de Queiroz, 1988; Lang, 1989).—(0) trapezoidal; (1) V or Y-shaped (posteriorly directed crest not developed); (2) Y-shaped with posteriorly directed median crest developed postembryonically; (3) Y-shaped with median crest developed embryonically; roofed at proximal end. Anoles have been treated as "unknown" because we regard the assignment of either "0" or "1" to be ambiguous. The peculiar vaulted parietal shape of chameleons and the "helmeted" condition of some anoles are regarded as nonhomologous with either of the apomorphic conditions here hypothesized.

11. **Parietal foramen** (Etheridge and de Queiroz, 1988; Lang, 1989).—(0) at frontoparietal suture or in parietal; (1) entirely within the frontal. *Laemanctus* is coded as "unknown" because of interspecific variability. Because they lack a parietal foramen, chameleons are considered to be "unknown."

12. **Supratemporal** (de Queiroz, 1987; Etheridge and de Queiroz, 1988) (Fig. 2).—(0) mostly on the lateral or ventral surface of the supratemporal process of the parietal; (1) mostly on the medial surface of the supratemporal process of the parietal; (2) mostly in a groove in the ventral margin of the supratemporal process of the parietal. In addition to the two possible positions of the supratemporal described by the above authors, we add a third, found in *Liolaemus* and *Ctenoblepharys*. In these genera the supratemporal lies within a groove in the ventral margin of the supratemporal process of the parietal so all but its posterior extremity is hidden from medial and lateral view. As an individual variant in a few species of *Liolaemus*, the element is located within a groove on the lateral surface of the parietal. Because we cannot polarize this set of transformations (other than hypothesizing that "0" is plesiomorphic) we regard this transformation as unordered. Chameleons are coded as "unknown" because the supratemporal is a small splint on the mediocaudal edge of the ventral ramus of the squamosal and has lost entirely any connection with the parietal (Rieppel, 1981).

13. **Osseous labyrinth** (Etheridge and de Queiroz, 1988).—(0) low to moderate elevation of the osseous labyrinth above the general level

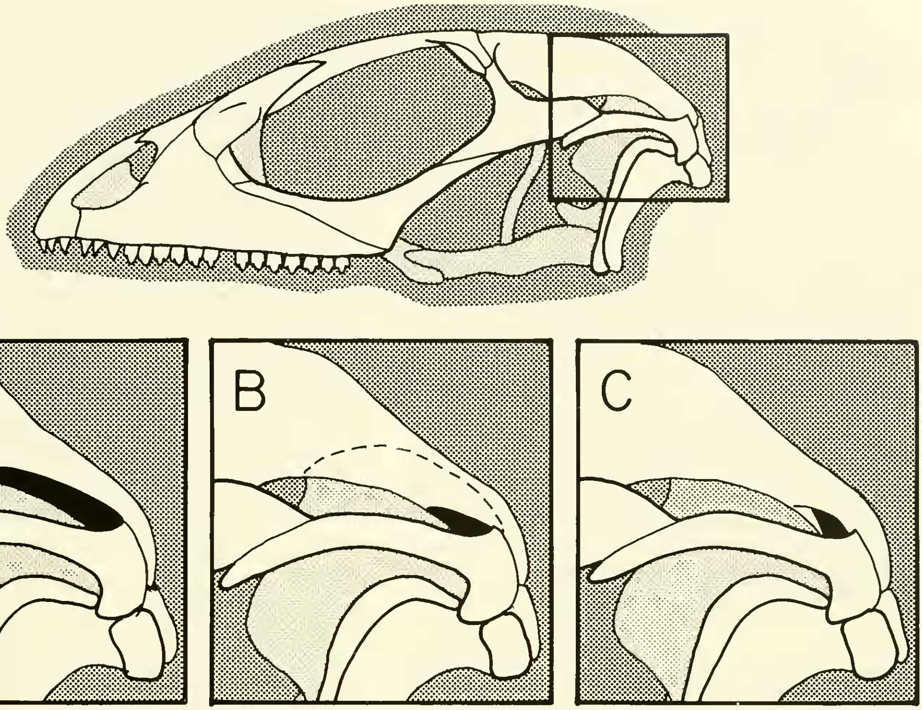

Fig. 2. Supratemporal position. A: supratemporal (in black) substantially on lateral side of supratemporal process of parietal. B: supratemporal substantially on medial side of supratemporal process of parietal (extent noted by dashed line). C: supratemporal fits in groove on ventral side of supratemporal process of parietal.

of the opisthotics; (1) high elevation above the general level of the opisthotics. Care must be taken in the evaluation of this feature because *all* very small iguanids have at least a moderately elevated labyrinth.

14. Endolymphatic sacs (Etheridge and de Queiroz, 1988).—(0) do not extend outside of otic capsule into nuchal musculature; (1) extend into nuchal musculature. Because some *Brookesia* (Moody, 1983b), the possible sister-taxon of other chameleons (Hillenius, 1986; Rieppel, 1987 [but see Klaver and Böhme, 1986]), have the apomorphic condition, chameleons have been coded as "unknown."

15. Epiotic foramen (Moody, 1980; Borsuk-Białynicka and Moody, 1984).—(0) absent; (1) present. Although Moody (1980) hypothesized that the otic depression in which the epiotic foramen sits is an apomorphy of slightly greater universality, the depression is difficult to characterize across all iguanian terminal taxa (i.e., it is reasonably well developed in all taxa that have elevated osseous labyrinths).

16. Dentary, expansion onto labial face of coronoid (Borsuk-Białynicka and Moody, 1984) (Fig. 3).—(0) dentary does not extend onto labial face of coronoid; (1) dentary extends onto labial face of coronoid. Out-group ambiguity ("1" in rhynchocephalians, "0" in most scleroglossans) requires that this transformation be treated as unpolarized.

17. Dentary, posterior extent (Pregill, 1984; Etheridge and de Queiroz, 1988) (Fig. 3).—(0) not or only moderately extending posteriorly beyond level of superior apex of coronoid; (1) extending posteriorly well beyond apex of coronoid. Because rhynchocephalians have condition "1" and scleroglossans "0," this transformation is treated as unpolarized. "*Tropidurus*" is coded as "unknown" because of interspecific variability (those west of the Andes have "0"; east of the Andes, they have "1"). Individual and interspecific variation does not allow further division of this transformation.

18. Coronoid labial blade (Etheridge, 1966; Etheridge and de Queiroz, 1988) (Fig. 3).—(0)

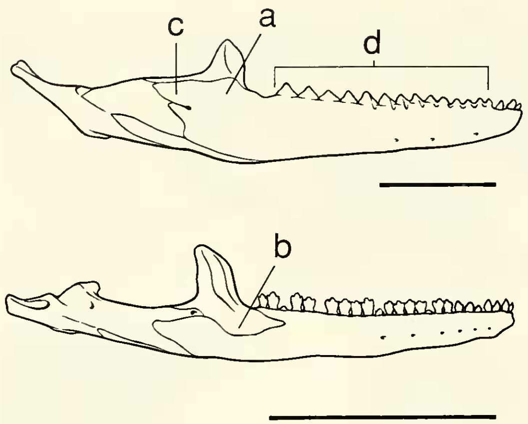

Fig. 3. Labial view of mandibles. Top: *Physignathus lesueuri*, KU 69303 (scale=10 mm). Bottom: *Leiocephalus carinatus*, UMMZ 149104 (scale=10 mm). Lettered arrows show: (a) dentary extending onto labial face of coronoid (Char. 16.1); (b) coronoid labial blade; (c) dentary extending posterior and superior to anterior surangular foramen (Char. 19.1); (d) fused, acrodont teeth (26.1).

present, large; (1) small or absent. Out-group ambiguity ("1" in many scleroglossans and rhynchocephalians; "0" in most scleroglossans) requires that this transformation be treated as unpolarized. Recognition of intermediate steps in this transformation are obviated by intraspecific variation.

19. Anterior surangular foramen (Fig. 3).—(0) anterior surangular foramen posterior to, or dorsal to posterior extremity of dentary; (1) anterior surangular foramen ventral to posterior extremity of dentary. In morunasaurs and acrodonts, the dentary extends posteriorly above the anterior surangular foramen. Because rhynchocephalians also have this condition, out-group ambiguity requires that this transformation be treated as unpolarized.

20. Meckel's groove (Etheridge and de Queiroz, 1988) (Fig. 4).—(0) not fused; (1) fused. Out-group ambiguity ("0" in rhynchocephalians; "1" or "0" in scleroglossans) requires that this transformation be treated as unpolarized. The apparently plesiomorphic condition in two Pleistocene species of *Leiocephalus* is regarded as a reversal (G. Pregill, pers. comm.). *Chalarodon madagascariensis* is individually variable and is coded as "unknown." Characterization of *Phymaturus*, *Oplurus*, *Liolaemus*, and *Basiliscus* is ambiguous because of interspecific variation; they are coded as "unknown."

21. Splenial, anterior extent (Fig. 4).—(0) extends anteriorly to or beyond ½ length of tooth row; (1) does not extend anteriorly more than ½ length of tooth row; (2) does not extend anteriorly more than ⅙ length of tooth row. This transformation series reflects the reduction of the splenial anteriorly. Because rhynchocephalians lack a splenial (Evans, 1980, 1981; Estes *et al.*, 1988) this transformation must be considered unpolarized. We are unaware how previous authors determined the identity of the angular (or angulosplenial?) in rhynchocephalians. *Oplurus* and *Liolaemus* are sufficiently variable interspecifically that we have coded them as "unknown."

22. Splenial, posterior extent (Fig. 4).—(0) terminates posteriorly anterior to anterior edge of mandibular fossa; (1) terminates posterior to, or at anterior edge of mandibular fossa. See comment under previous transformation series. Because of out-group ambiguity, this transformation series must be considered unpolarized. "*Enyalioides*" is coded as "unknown" because of in-group variability ("1" in "*E.*" *laticeps*; "0" in other morunasaurs). *Corytophanes* is also coded as "unknown" for the same reason ("0" in *C. percarinatus*; "1" in *C. hernandezi*).

23. Angular, condition of contact with splenial (Etheridge and de Queiroz, 1988) (Fig. 4).—(0) angular large; suture with splenial on lingual face; (1) angular small; suture with splenial on ventral or labial face. Because rhynchocephalians lack a splenial, this transformation series must be treated as unpolarized. *Oplurus* is coded as "unknown" because of interspecific variation.

24. Posterior mylohyoid foramen (Fig. 4).—(0) anterior to or approximately at the level of superior apex of coronoid; (1) between level of superior apex of coronoid and anterior end of adductor fossa; (2) posterior to anterior end of adductor fossa. In rhynchocephalians and *Uromastyx*, the posterior mylohyoid foramen appears to be united with the widely open Meckel's groove. In scleroglossans, the posterior mylohyoid foramen is anterior to the level of the peak of the coronoid. Therefore, any posterior placement

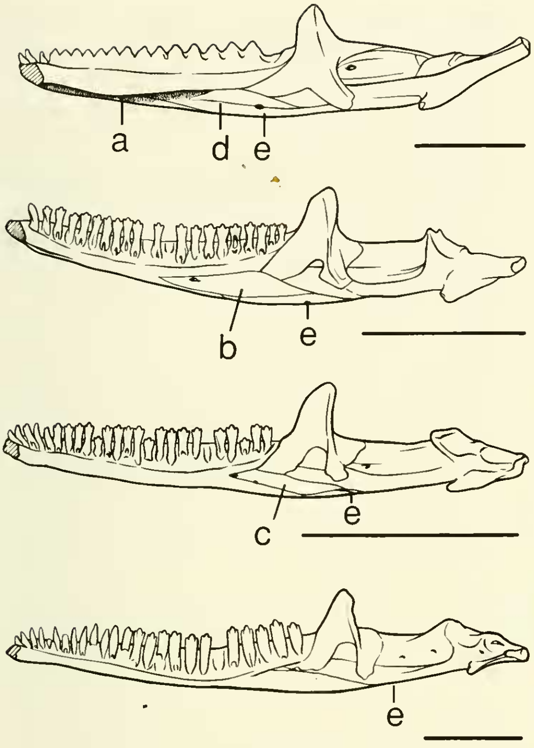

Fig. 4. Lingual view of mandibles. Top: *Physignathus lesueuri*, KU 69303 (scale=10 mm). Middle top: *Basiliscus basiliscus*, KU 93452 (scale=10 mm). Middle bottom: *Leiocephalus carinatus*, UMMZ 149104 (scale=10 mm). Bottom: *Anolis petersi*, KU 187446 (scale=10 mm). Lettered arrows show: (a) unfused Meckel's canal (Char. 20.0); (b) splenial extending to or beyond ½ length of tooth row (Char. 21.0); (c) splenial extending less than ⅙ length tooth row (Char. 21.2); (d) angular contacting splenial on lingual face (Char. 23.0); (e) position of posterior mylohyoid foramen (Char. 24).

of this foramen is considered derived. *Petrosaurus* and *Oplurus* are coded as "unknown" because of interspecific variability ("1" and "2").

25. Crowns of marginal teeth (de Queiroz, 1987; Etheridge and de Queiroz, 1988).—(0) not polycuspate; (1) polycuspate. Variation in the shape of the crowns of the teeth is bewildering, except for this transformation. Although *Brachylophus* is variably polycuspate (and then weakly) it has been coded as polycuspate (de Queiroz, 1987).

26. Posterior maxillary and dentary teeth (Camp, 1923; Cooper *et al.*, 1970; Estes *et al.*, 1988) (Fig. 3).—(0) pleurodont, replaced; not fused to underlying bone; (1) acrodont, not replaced as adults; fused to underlying bone. Because †*Gephyrosaurus* (the earliest rhynchocephalian) does not have fused, acrodont teeth, the acrodontan and rhynchocephalian conditions are not considered homologous.

27. Palatine teeth (Moody, 1980; Etheridge and de Queiroz, 1988).—(0) present; (1) absent. Because of out-group ambiguity ("1" or "0" in Scleroglossa; "0" in rhynchocephalians) this transformation must be considered unpolarized. *Oplurus* is coded as "unknown" because of interspecific variability.

28. Pterygoid teeth (Moody, 1980; Etheridge and de Queiroz, 1988).—(0) present; (1) absent. *Polychrus* and *Leiocephalus* are coded as "unknown" because of interspecific variability.

29. Ceratobranchials (Etheridge and de Queiroz, 1988).—(0) second not reaching clavicles; (1) second reaching clavicles. Chameleons are considered "unknown" because ceratobranchials are lacking.

30. Clavicle (Moody, 1980; Etheridge and de Queiroz, 1988).—(0) flat, with wide lateral flange; (1) flange small or absent. Because the clavicular flange is variably present in the outgroups, the polarity of this transformation must be considered unknown. Anoles and *Liolaemus* are coded as "unknown" because of interspecific variability. Chameleons are coded as "unknown" because they lack clavicles.

31. Insertion of clavicle (Lang, 1989).—(0) on suprascapula; (1) on scapula. Anoles are coded as "unknown" because of interspecific variability. Chameleons are coded as "unknown" because they lack clavicles. We have treated this transformation as unpolarized because rhynchocephalians have condition "1" (Evans, 1981).

32. Interclavicle (Camp, 1923; Etheridge, 1966; Lécuru, 1968; Moody, 1980).—(0) anterior process absent; (1) anterior process well developed. This transformation is treated as unpolarized because rhynchocephalians lack the anterior process, whereas scleroglossans have it plesiomorphically. Chameleons are assigned an "unknown" because they lack an interclavicle.

33. Sternum, anterior extent (Fig. 5).—(0) sternum does not approach junction of posterior and lateral processes of interclavicle closely; (1) sternum approaches junction of lateral and poste-

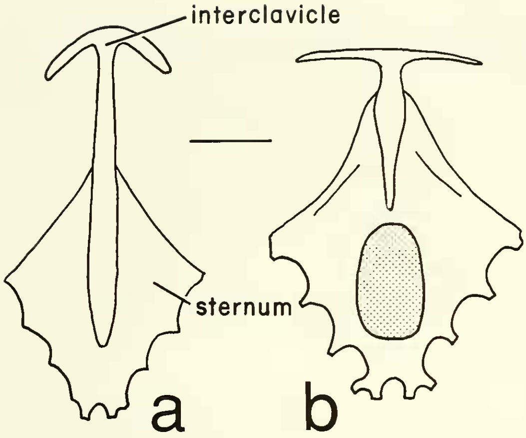

Fig. 5. Sterna and interclavicles. (a) *Dipsosaurus dorsalis*, KU 69107; sternum does not approach juncture of posterior and lateral processes of interclavicle (Char. 33.0). (b) *Plica plica*, M. A. Norell 76; sternum extends to juncture of posterior and lateral processes of interclavicle (Char. 33.1).

rior processes of interclavicle closely. In some iguanids the sternum extends anteriorly almost all the way to the junction of the posterior and lateral processes of the interclavicle. The more widespread condition, found in the out-groups, is for the posterior process of the interclavicle to be free for a significant part of its length.

34. Caudal vertebral type (Etheridge, 1967; Etheridge and de Queiroz, 1988).—(0) *Sceloporus* condition (transverse processes anterior to fracture plane [if present], transverse processes extend far down length of tail); (1) *Iguana* condition (fracture plane passes between paired transverse processes); (2) *Basiliscus* condition (transverse processes generally not present, in anomalous conditions when present they are anterior to fracture plane); (3) anole condition (transverse processes, if present, posterior to fracture planes). Because of out-group comparison problems, these characters must be regarded as unordered with respect to each other. *Polychrus*, lacking fracture planes, could be either condition "2" or "3," and is therefore coded as "unknown." Para-anoles are coded as "unknown" because they could be considered "0" or "3."

35. Scapular fenestra (Etheridge and de Queiroz, 1988).—(0) present; (1) absent. Outgroup comparison is ambiguous; that is, scleroglossans are variable in the presence or absence of a scapular fenestra, although rhynchocephalians clearly lack them. For this reason, this transformation is considered to be unpolarized. *Polychrus* is coded as "unknown" because of interspecific variability. "*Enyalioides*" is coded as "unknown" because of deductive limitations ("1" in "*E.*" *laticeps*; "0" in other morunasaurs). Chameleons are coded as "unknown" because of interspecific variability and dubious homology of the fenestrations.

36. Posterior coracoid fenestra (Etheridge and de Queiroz, 1988).—(0) present; (1) absent; (2) marginal and weak. Out-group comparison is ambiguous (i.e., scleroglossans are variable, even though rhynchocephalians clearly lack coracoid fenestrae). Therefore, this transformation is considered unordered. However, many iguanids that "lack" this fenestra have a thin area of bone in the shape of this fenestra, which implies to us that presence is the plesiomorphic condition within Iguania. The leiosaurs and para-anoles share the condition of having a small, peculiar, marginal fenestra in the position of a posterior coracoid fenestra (condition "2"). Because we lack any clear justification for the polarity between conditions "1" and "2," we have considered this transformation to be unordered.

37. Median enlarged sternal fontanelle(s) (Etheridge, 1964; Moody, 1980; Etheridge and de Queiroz, 1988).—(0) absent or small, often hidden by interclavicle; (1) present, large, and not paired; (2) present, large and paired. Although "0" clearly is the plesiomorphic condition, "1" and "2" are arguably polarized. Therefore, these characters are treated as unordered with respect to each other.

38. Cervical ribs (Etheridge, 1964; Moody, 1980; Etheridge and de Queiroz, 1988).—(0) first pair on vertebra number 3; (1) first pair on vertebra number 4; (2) first pair on vertebra number 5. This transformation is considered unpolarized because of ambiguous out-group comparison. *Liolaemus*, *Enyalius*, and "*Pristidactylus*" are coded as "unknown" because of interspecific variability. Chameleons are coded as "unknown" because numerical homology of the cervical vertebrae cannot be determined.

39. Number of sternal ribs (Etheridge and de

Queiroz, 1988).—(0) four; (1) three; (2) two or fewer. *Liolaemus* is coded as "unknown" because of interspecific variability (3 or 4 ribs), as are anoles (3 or 2 ribs).

40. Postxiphisternal inscriptional ribs (Etheridge, 1965; Etheridge and de Queiroz, 1988).—(0) all attached proximally to dorsal ribs and none are confluent midventrally; (1) one or more pairs attached to dorsal ribs and are confluent midventrally; (2) none attached to dorsal ribs or continuous midventrally; present as pairs of isolated elements. Although "0" is clearly plesiomorphic, the polarity of "1" to "2" cannot be determined. Therefore, this transformation series is considered unordered.

41. Tail autotomy fracture planes (Estes *et al.*, 1988; Etheridge and de Queiroz, 1988).—(0) present; (1) absent. *Uromastyx* is assigned an "unknown" because at least some specimens of *U. acanthinurus* have functional fracture planes (Etheridge, pers. observ.). *Enyalius* and anoles are coded as "unknown" because of interspecific variability.

42. Interparietal scale (Smith, 1946; Etheridge and de Queiroz, 1988).—(0) small (or absent); (1) large; as wide as interorbital space. Sand lizards have been assigned an "unknown" because of in-group variability (i.e., *Uma* has a small interparietal). In spite of our coding, on anatomical grounds it is questionable whether the enlarged interparietal of sceloporines is homologous with the "enlarged" interparietal found in some tropidurines; particularly in *Uranoscodon* and "*Tropidurus*" west of the Andes, evidence of edge-to-edge fusion of scales is frequently obvious.

43. Interparietal coloration (Etheridge, 1969a).—(0) black spot absent; (1) black spot present. Although the apomorphic condition appears in some other iguanian species (e.g., *Sceloporus nelsoni*), it is not ancestral in any other terminal taxon except the oplurines.

44. Superciliary scales (Etheridge and de Queiroz, 1988).—(0) distinctly elongate and imbricate; (1) not distinctly elongate and imbricate. Ambiguous out-group comparison (*Sphenodon* has condition "1," but scleroglossans are not really comparable) requires use of this transformation as non-polarized. Because of interspecific variation, *Phymaturus* is coded as "unknown."

45. Subocular scale (Etheridge and de Queiroz, 1988).—(0) at least one scale below the eye conspicuously enlarged; (1) scales below the eye subequal. Out-group comparison does not support a particular polarity of this transformation; it is therefore considered as unpolarized (*Sphenodon* has subequal subocular squamation; scleroglossans are variable). Because of interspecific variability ("0" in *E. bilineatus*; "1" in other species), *Enyalius* is coded as "unknown" as are the para-anoles ("0" in *Anisolepis*; "1" in *Urostrophus**), *Liolaemus*, and *Phymaturus* ("0" in *P. patagonicus*; "1" in *P. palluma*).

46. Mid-dorsal scale row (Etheridge and de Queiroz, 1988; Estes *et al.*, 1988).—(0) present; (1) absent. We have not addressed differences of development of the median dorsal crest because of complex intra- and interspecific variation. *Polychrus* and anoles are considered "unknown" because of interspecific variation. Because of out-group ambiguity ("0" in *Sphenodon*; "1" in Scleroglossa) this transformation is treated as unpolarized.

47. Gular fold (Etheridge and de Queiroz, 1988).—(0) complete medially; (1) incomplete medially or absent. Because some species (e.g., *Polychrus femoralis*) have "gular folds" that lack any kind of distinctive change in squamation at the fold line, we have restricted the use of "gular fold" to those species that have a distinct change in squamation at the level of the fold. For this reason, the condition found in *Polychrus femoralis* is considered "1" and the condition in *Laemanctus* is considered "0."

48. Femoral pores (Camp, 1923; Etheridge and de Queiroz, 1988).—(0) present; (1) absent. Out-group ambiguity (*Sphenodon* lacks femoral pores but Scleroglossa has them plesiomorphically) requires the treatment of this transformation as unpolarized, even though this feature has been considered a synapomorphy of Squamata (Kluge, 1983; Gauthier *et al.*, 1988).

49. Preanal pores (Laurent, 1984; Etheridge and de Queiroz, 1988).—(0) absent; (1) present.

50. Distal subdigital scales (Etheridge and de Queiroz, 1988).—(0) undivided; (1) divided. Although *Sphenodon* lacks regular subdigital scales, it clearly lacks the apomorphic condition here specified, and is therefore regarded as having condition "0."

51. Subdigital scale surface macrostructure (Peterson and Williams, 1981; Etheridge and de Queiroz, 1988).—(0) carinate; (1) smooth. Outgroup ambiguity (*Sphenodon* has smooth subdigital scales even though scleroglossans usually have carinate subdigitals) requires the treatment of this transformation as unpolarized. Chameleons, *Enyalius,* and "*Pristidactylus*" are coded as "unknown" because of interspecific variation.

52. Scale organs (Peterson, 1983; Etheridge and de Queiroz, 1988; E. E. Williams, pers. comm.).—(0) spinules absent; (1) spinules present. We have simplified the transformation series of Etheridge and de Queiroz (1988) in order to obviate some out-group comparison problems. Chameleons are assigned an "unknown" because of interspecific variation.

53. Nasal chamber, sink trap (Stebbins, 1948).—(0) primitive condition (short vestibule, concha well developed) or some apomorphic condition not homologous with Character 53.1; (1) sink-trap (elongate septomaxilla) (condition #1 of following discussion).

Malan (1946), in her study of the comparative anatomy of the lacertilian nasal capsule, provided a solid framework to which other contributions were made by Stebbins (1948) and Stimie (1966). Although Malan's work was the most detailed, for purposes of this discussion we use the nomenclature and points of reference of Stebbins (1943, 1948) because his work is most directly applicable to our own observations.

Primitively, saurians have a relatively long vestibule leading from the external naris to the nasal cavity. This vestibule is lined with erectile tissue (Lapage, 1926; Malan, 1946), which has been hypertrophied to form nasal valves in various lineages. The vestibule attaches anterodorsally to the nasal cavity, which is divided sagittally by a "tongue" of tissue, the *concha*, that projects medially into the nasal cavity. More or less hidden from dorsal view, beneath the concha, the slit-like internal nares communicate with the oral cavity. Behind the internal choana and the concha is a blind cavity, the antorbital chamber. This condition obtains in *Sphenodon* and in various degrees of modification in most scleroglossans.

In iguanians there are five major deviations from this pattern (discussed under subsequent transformation series): (1) sink-trap; (2) "S" condition; (3) fusion of nasal concha to chamber roof (=reduction of supraconchal part of nasal chamber); (4) anole condition; (5) acrodontan condition.

The sink-trap nasal apparatus of the sceloporines seems to have been derived from the primitive condition by more or less direct posterior elongation of the vestibule (which is supported by an equally apomorphic elongate septomaxilla) to enter the nasal cavity at the posterodorsal end.

54. Nasal chamber, S-condition (Stebbins, 1948).—(0) primitive condition, or apomorphic condition not homologous with Character 54.1; (1) S-condition (septomaxilla plow-share shaped) (condition #2 of discussion under "Transformation Series 53"). In the S-condition the vestibule is elongate, S-shaped, and overlies the nasal cavity. In all cases, the septomaxilla extends dorsally to contact the osseous roof of the nasal cavity, and is shaped like a plow-share, a condition otherwise unknown in lizards. Phylogenetically, we hypothesize that the S-condition was derived from the primitive condition by simple elongation of the vestibule over the nasal cavity, whereby the vestibule opens into the nasal cavity dorsomedially rather than in the primitive anterodorsal position.

55. Nasal chamber, fusion of nasal concha to roof of nasal chamber.—(0) primitive condition, or other apomorphic condition not homologous with Character 55.1; (1) fusion of concha to roof of nasal chamber. In the "*Stenocercus*" and the "*Tropidurus*" groups the primitive condition is largely retained, except that the concha is fused to the roof of the nasal chamber (condition #3 of discussion under "Transformation Series 53"). In some species, the vestibule is slightly elongated and enters the nasal chamber at a relatively high level.

56. Nasal chamber, anole condition (Stebbins, 1948).—(0) primitive condition, or some apomorphic condition not homologous with Character 56.1; (1) nasal concha lost, with nasal chamber otherwise retaining plesiomorphic organization (condition #4 in discussion under "Transformation Series 53"). In *Anolis*, and presumably their near relatives, the concha is lost (Malan, 1946; Stimie, 1966), although otherwise the plesiomorphic condition is maintained. The concha also is missing in *Polychrus*, but present (although weak) in *Diplolaemus* and "*Pristidactylus*." Para-anoles and *Enyalius* are coded as "unknown" because rarity in museum collections precludes dissection.

57. Nasal chamber, acrodontan condition (Malan, 1946; Parsons, 1970; Słaby, 1981, 1984).—(0) primitive nasal condition, or some apomorphic condition not homologous with Character 57.1; (1) reduction of concha concomitant with elongation of the nasal vestibule (condition #5 in discussion under "Transformation Series 53"). Agamidae* (except *Physignathus* which has the primitive iguanian pattern of having a relatively short nasal vestibule and a small nasal concha) and chameleons have an unusual condition in which there is a long vestibule extending from a lateral or dorsolateral naris over the nasal chamber and enters the nasal chamber posterodorsally (Parsons, 1970). The nasal concha is very small (*Leiolepis*) or absent (e.g., *Uromastyx*, "*Agama*," chameleons). In some aspects, the acrodontan condition is intermediate between the "S" condition and the sink-trap, but the unusual septomaxillary anatomy in all three conditions (very long in the sink-trap; plowshare shaped in the "S" condition; and very small or absent in the acrodontan condition) argue for nonhomology. Chameleons have modified the agamid condition in a number of ways that seem to be correlated with enlargement of the eyes and tongue (Malan, 1946).

58. Ulnar nerve pathway (Jullien and Renous-Lécuru, 1972; Renous, 1979; Estes, 1983a; Etheridge and de Queiroz, 1988).—(0) L-condition (superficial); (1) V-condition (deep). Out-group ambiguity requires use as unpolarized.

59. Dorsal shank muscle innervation (Jullien and Renous-Lécuru, 1972; Renous, 1979; Etheridge and de Queiroz, 1988).—(0) A-condition (peroneus); (1) B-condition (interosseus). Out-group ambiguity requires use as unpolarized.

60. Hemipenis, posterior lobe (Fig. 6).—(0) no enlarged posterior lobe; (1) enlarged posterior

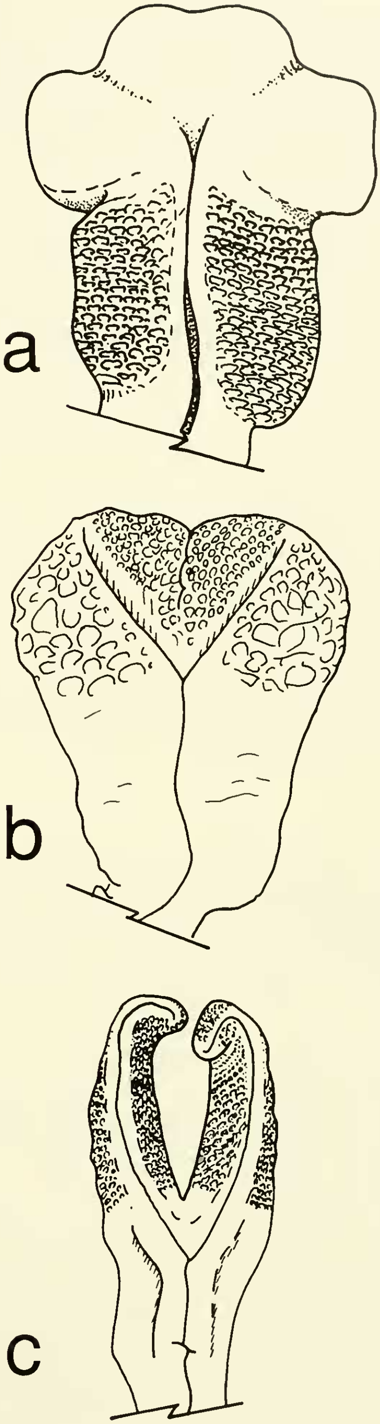

Fig. 6. Hemipenes. (a) *Sceloporus torquatus*, KU 91414, showing enlarged posterior lobe (Char. 60.1). (b) "*Stenocercus*" *festae*, KU 134588, showing bilobate, bisulcate condition (Char. 61.1). (c) *Plica umbra*, KU 147946, showing bicapitate, bisulcate condition (Char. 61.2).

lobe. In sceloporines, a posterior eminence, normally present but small in other lizards, is enlarged to the point that in superficial examination of the sceloporine hemipenis it seems to have a posterior median lobe. Because *Sphenodon* lacks a hemipenis, this transformation must be regarded as unpolarized.

61. Hemipenis, capitation and sulci (Fig. 6).—(0) unicapitate or weakly bilobate without distinctly divided sulci; (1) bilobate with distinctly divided sulci; (2) strongly bicapitate. The only members of the first out-group similar enough to be comparable, teiids, support the polarity 0→1→2. However, because *Sphenodon* lacks a hemipenis, this transformation must be regarded as unpolarized.

62. Hemipenis, *m. retractor lateralis posterior* (Arnold, 1984).—(0) not completely divided; (1) completely divided. Because *Sphenodon* lacks a hemipenis, this transformation must be regarded as unpolarized.

63. Hemipenis, *m. retractor lateralis posterior* (Arnold, 1984).—(0) not substantially situated within the hemipenial sheath; (1) substantially situated within the hemipenial sheath. Because *Sphenodon* lacks a hemipenis, this transformation must be regarded as unpolarized.

64. Hemipenis, dorsal accessory sheath muscle (Arnold, 1984).—(0) absent; (1) present. Because *Sphenodon* lacks a hemipenis, this transformation must be regarded as unpolarized.

65. Colic septa (Lönnberg, 1902; El Taubi and Bishai, 1959; Iverson, 1980, 1982).—(0) absent; (1) present. Agamas are coded as "unknown" because of the presence of colic septa in *Hydrosaurus*.

66. Paired ventrolateral belly patches in males (Etheridge and de Queiroz, 1988).—(0) absent; (1) present. "*Stenocercus*" is coded as "unknown" because some large-scaled species (e.g., "*S.*" *rhodomelas*) have paired ventrolateral patches.

67. Reticular papillae on tongue (Schwenk, 1988).—(0) absent; (1) present. Because we depended entirely on the literature for this transformation (suggested to be synapomorphy of anoles and acrodonts), a number of taxa had to be coded as "unknown."

RESULTS

A total of 225 alternative supported (as opposed to unrejected) tree topologies were discovered (208 steps; C.I.=0.385). Twelve networks were discovered that could be variously rooted to produce 18 unique trees of nine major monophyletic groups (acrodonts; anoloids; basiliscines; crotaphytines; iguanines; morunasaurs; oplurines; sceloporines; and tropidurines) (Fig. 7). Within these monophyletic groups alternative topologies exist that are variously independent to dependent on intergroup topology. Within the *Liolaemus* group of the tropidurines two topologies were discovered, three in the sceloporines, two in the acrodonts, and three in the anoloids.

A strict consensus tree (Nelson, 1979) of the discovered tree topologies is presented in Figure 8. This consensus tree is not a parsimonious solution of the data, but only a figure showing the commonalities among the discovered trees. The extensive polytomies seen in the consensus tree are due both to variation in rooting points within networks and topological differences among equally parsimonious unrooted networks. Regardless of the impression given by the consensus tree, not all of the phylogenetic trees logically consistent with the strict consensus tree are, in fact, allowed within the constraints of the discovered network topologies. Many trees are excluded (e.g., those showing a sister-taxon relationship between acrodonts and crotaphytines). If attainment of a single tree is the only measure of progress in the understanding of iguanian relationships, we have failed egregiously. However, the number of possible dichotomous trees for 35 in-group taxa is 4.89 x 10^{47} (Felsenstein, 1978). Because we have rejected all but 549 dichotomous 208-step trees (i.e., all but 1.12 x 10^{-45}% of the total possible), we consider that we have made great progress, indeed.

It is clearly impossible because of space considerations to discuss the character support for each topology. Therefore, only evidence for major monophyletic groups and organization within them will be discussed. In order to docu-

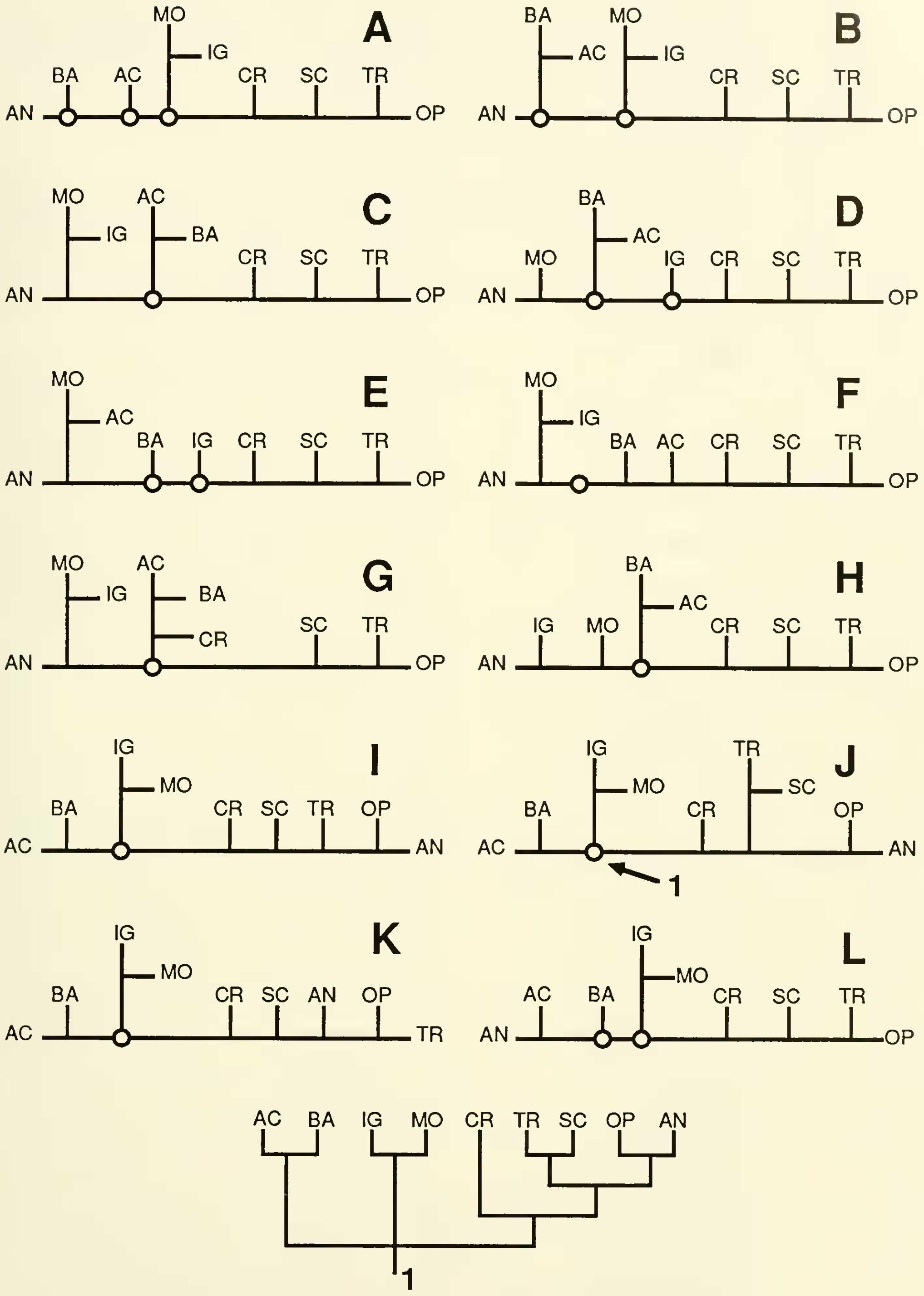

Fig. 7. Discovered unrooted networks with discovered rooting points (-o-). AC=acrodont groups (agamines, uromastycines, and chameleons); AN=anoloids; BA=basiliscines; CR=crotaphytines; IG=iguanines; MO=morunasaurs; OP=oplurines; SC=sceloporines; TR=tropidurines. Arrow points to rooting point (position of ancestor vector) that results in tree 1.

ment the degree of homoplasy required by all discovered trees, one tree, arbitrarily selected, is completely documented in Figure 9 and Appendices 2 and 3.

ACRODONTS

As expected, Agamidae* and Chamaeleonidae together form a monophyletic group, although two topologies were discovered (Fig. 10). Topology 1 was discovered in intergroup Networks A–D and F–K, but Topology 2 was discovered only in Networks B, E, and L (Fig. 7).

Topology 1.—The monophyly of the agama operational taxonomic unit (=agamids, excluding *Physignathus, Uromastyx,* and *Leiolepis*) may be supported by 32.1 (well-developed anterior process of interclavicle), however, the interclavicle is lost in chameleons and is unknown in †*Priscagama**. Therefore, the alternative must be entertained that 32.1 is plesiomorphic in this clade with a reversal in *Leiolepis* and *Physignathus*. *Physignathus* apparently has a reversal to 30.0 (flat clavicle with a wide lateral flange) although this is also an ambiguous placement because the clavicle is absent in chameleons and unknown in †*Priscagama**. Stem 1 (agamas + *Physignathus*) is corroborated by 15.1 (epiotic foramen) and is in agreement with the results of Moody (1980). Also, 31.1 (insertion of clavicle on scapula) may belong here, but placement is made ambiguous by the lack of a clavicle in chameleons and being unknown in †*Priscagama**. Chameleon monophyly is supported by a number of characters that are apomorphies in all topologies: 39.2 (strong reduction of number of sternal ribs), 47.1 (loss of gular fold), 48.1 (loss of femoral pores), and 58.1 (V-condition of ulnar nerve pathway). In the networks that support this topology, 7.1 (extensive skull rugosity) and 40.1 (midventrally confluent postxiphisternal inscriptional ribs) also are apomorphic.

Stem 2 carries unambiguously only one character that supports the monophyly of the chameleons + agamids, excluding *Leiolepis* and *Uromastyx*: 6.1 (extremely enlarged lacrimal foramen). Although this condition as characterized is shared with morunasaurs, both chameleons and agamids (other than the uromastycines) have these foramina more enlarged than in moruna-

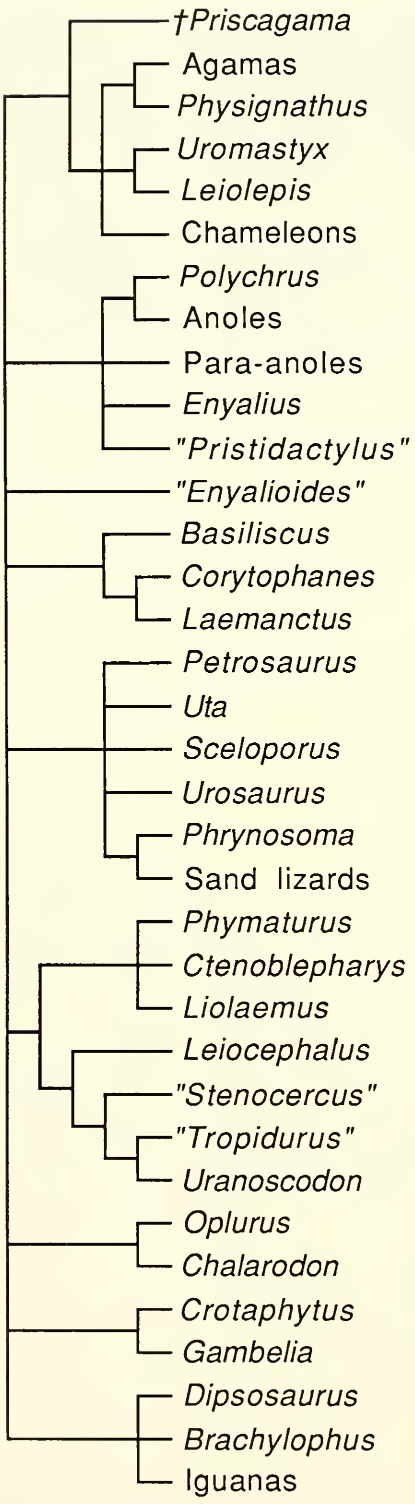

Fig. 8. Strict consensus tree (Nelson, 1979) of terminal taxa.

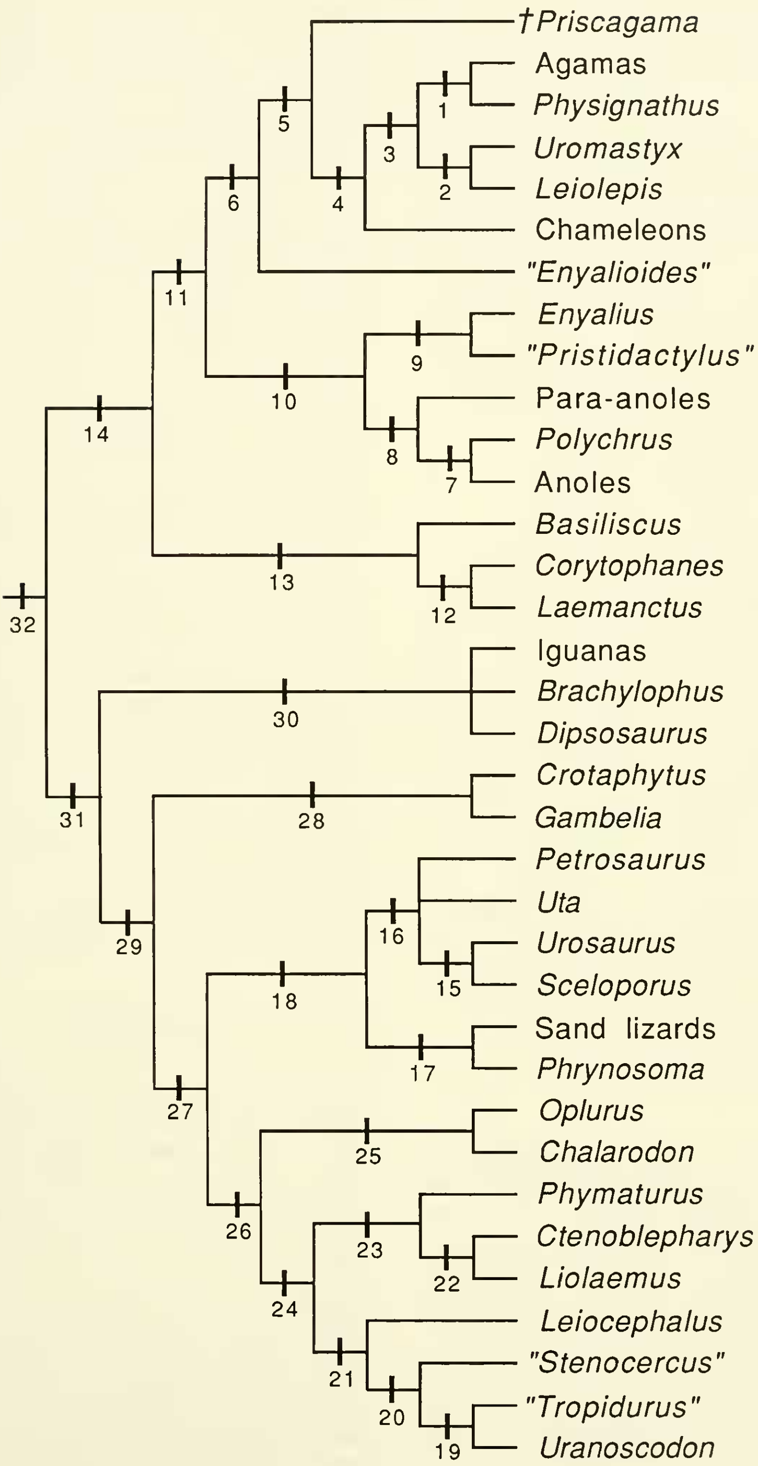

Fig. 9. A 208-step tree selected arbitarily from among those discovered. Character shifts for this tree are documented in Appendices 2 and 3.

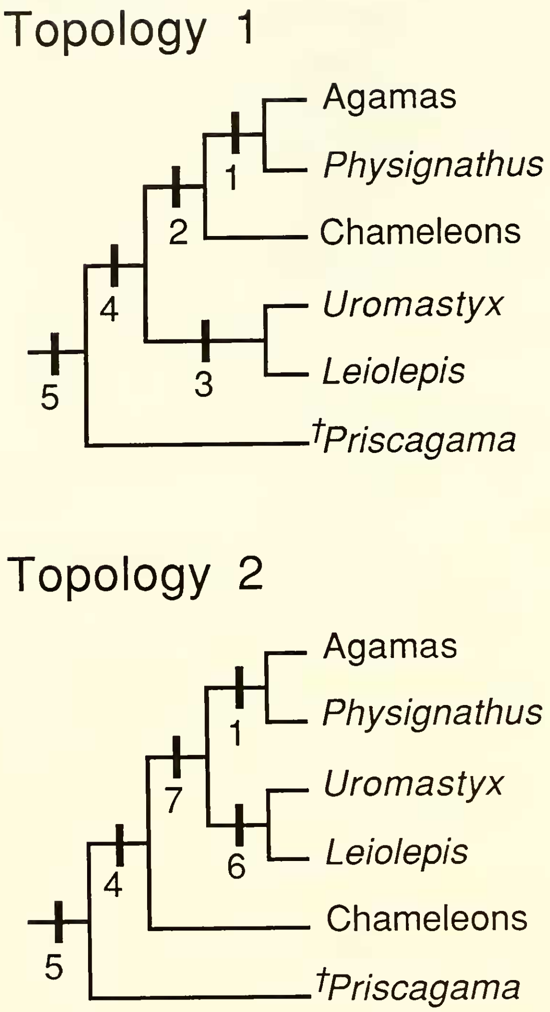

Fig. 10. Alternative topologies discovered for the acrodont groups.

saurs and extremely enlarged in contrast to the condition found in uromastycines, which have the primitive condition. Another character that "falls out" on this stem is 39.1 (reduction of sternal ribs from 4 to 3), although in some topologies this is made ambiguous by the sternal rib number being unknown in †*Priscagama**.

The monophyly of *Uromastyx* is supported by: 5.1 (loss of the lacrimal) and 65.1 (appearance of colic septa—also in *Hydrosaurus* and iguanines). Character 36.0 (anterior process of interclavicle) is placed here ambiguously; see previous discussion. *Leiolepis* is corroborated by 62.1 (completely divided *m. retractor lateralis posterior*). Stem 3 (uniting *Leiolepis* and *Uromastyx*) is supported by only one unique, unreversed character, 4.1 (cup-shaped vomers), although in some arrangements three other features "fall out" on this stem: 3.0 (reduction of posterior extent of maxilla), 39.0 (four sternal ribs), and 46.1 (mid-dorsal enlarged dorsal scale row). 3.0 is rendered ambiguous by variation within chameleons, 39.0 is rendered ambiguous by network topology, and 46 is rendered ambiguous by being unknown in †*Priscagama**.

Stem 4 (acrodonts above †*Priscagama**) is supported by three unambiguously placed apomorphies: 16.1 (expansion of dentary onto labial face of coronoid), 17.1 (far posterior extension of the dentary), 21.1 (shortening of the splenial), and 28.1 (loss of pterygoid teeth).

†*Priscagama** has no unambiguously placed apomorphies. Stem 5 (the acrodont groups), as noted in "Choice of Terminal Taxa," is well-corroborated by 2.1 (maxillae meet anteromedially behind palatal portion of the premaxilla) and 26.1 (acrodont maxillary and dentary teeth, fused in adults). Additionally, several characters of ambiguous placement may belong on this stem: 3.1 (posterior extent of maxilla posterior to frontoparietal suture) is variable in chameleons and likely reversed in *Uromastyx* and *Leiolepis*; 9.1 (postfrontal reduced) in some topologies is of greater universality; 19.1 (anterior surangular foramen ventral to posterior extremity of dentary) in some topologies has a greater level of universality (shared with morunasaurs); 37.1 (large, paired sternal fontanelles) is ambiguous because it is unknown in †*Priscagama** and because of the extreme sternal modification in chameleons; 57.1 (acrodontan nasal condition [reversed in *Physignathus*]) and 67.1 (reticular lingual papillae) are also unknown in †*Priscagama**.

Topology 2.—Agamas, *Physignathus*, chameleons, *Uromastyx*, *Leiolepis*, and stems 4 and 5 are as in Topology 1. Stem 6 (*Leiolepis* + *Uromastyx*) in this topology is nearly the same as Stem 3 as in Topology 1, except that the lacrimal foramina (6.0) are secondarily reduced (enlargement being an apomorphy of possible extra-acrodont universality). Stem 7, supporting a monophyletic Agamidae, carries 37.2 (paired, enlarged sternal fontanelles), although this is ambiguous because of strong modification of chameleon sterna and being unknown in †*Priscagama**, and a reversal to 40.0 (short postxiphisternal inscriptional ribs) that is dependent on the topology of the intergroup network.

For no reason other than the comparative rarity of topologies that allow the chameleons to form the sister-taxon of the remaining acrodonts, we suspect that chameleons are nested within the traditional Agamidae*.

There are, of course, some general iguanian topologies that do not preclude the acrodont taxa, Agamidae* and Chamaeleonidae, from forming the sister-taxon of Iguanidae* (Fig. 7). In these trees no putative synapomorphies of Iguanidae* are unambiguously placed, and the characters that are placed ambiguously are all unordered or unpolarized characters that were assigned arbitrarily by the computer program: 19.0 (anterior surangular foramen posterior to, or dorsal to posterior extremity of dentary [Ancestor assigned 19.1—posterior mylohyoid foramen ventral to posterior extremity of dentary]), 30.0 (clavicular flange flat, with wide lateral flange [Ancestor assigned 30.1—clavicular flange reduced or absent]), 38.1 (posterior coracoid fenestra absent), and 63.1 (*m. retractor lateralis posterior* not substantially situated within the hemipenial sheath [Ancestor assigned 63.0]).

ANOLOIDS

The anoloid genera of Etheridge and de Queiroz (1988) formed a monophyletic group in all obtained trees and formed three topologies (Fig. 11). Additionally, because para-anoles do not have their monophyly supported unambiguously it is conceivable that *Urostrophus** and *Anisolepis* are more closely related to other anoloid genera than to each other. All three anoloid topologies differ from the cladogram presented by Etheridge and de Queiroz (1988), primarily in the placement of *Polychrus*. Etheridge and de Queiroz (1988) considered *Polychrus* to be the sister-taxon of other anoloids (on the basis of its having femoral pores and nonspinulate scale organs), whereas we consider it to be the sister-taxon of anoles. The change of placement apparently requires the reacquisition of femoral pores in *Polychrus* as well as the loss of an otherwise ubiquitous feature of anoloids, spinulate scale organs.

Topology 1 was discovered in Networks A–H (Fig. 7); Topology 2 was discovered in Networks A–B and E; and Topology 3 was discovered in Networks A–B, I–L (but not in A and B when rooted such that anoloids are in polytomy with the remaining iguanians). *Polychrus* was sup-

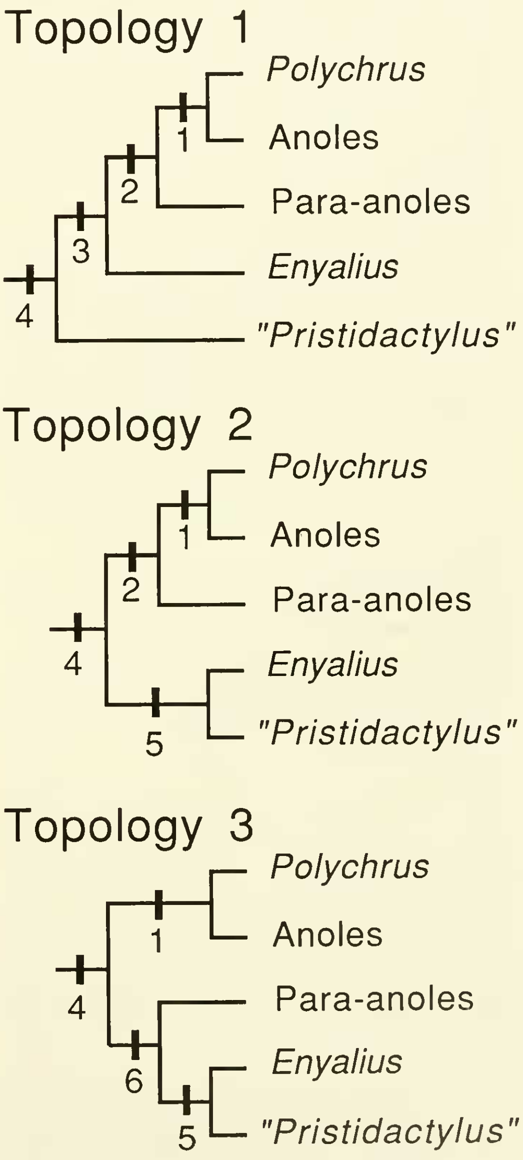

Fig. 11. Alternative topologies discovered within anoloids.

ported in all trees by three unambiguously placed characters: 5.1 (loss of lacrimal), 48.0 (regaining of femoral pores), and 52.0 (loss of spinulate scale organs). Additionally in Topologies 1 and 2, 27.1 (loss of palatine teeth) is placed on this stem. Regaining of carinate subdigital scales (51.0) possibly is a feature of *Polychrus*, but because this feature is variable in "*Pristidactylus*" and *Enyalius*, its placement is ambiguous.

The monophyly of anoles is supported by a number of features in all three topologies: 17.1 (far posterior extension of dentary), 18.0 (regaining of coronoid labial blade), 21.2 (little anterior extension of splenial), 23.1 (reduced angular), 24.2 (far posterior placement of posterior mylohyoid foramen), and 67.1 (reticular lingual papillae). Stem 1 (anoles + *Polychrus*) is corroborated by four unambiguously placed characters: 29.1 (second ceratobranchial extends to clavicles), 33.1 (anterior process of interclavicle), 38.2 (most anterior cervical ribs on vertebra 5), and 47.1 (loss of gular fold). Other, more ambiguously placed features possibly on this stem are: 30.1 (clavicular flange reduced), 31.1 (clavicular insertion on scapula), and 39.2 (≤ 2 sternal ribs), which are variable in anoles. Additionally, Ernest E. Williams (pers. comm.) has noted that *Polychrus* and the anoles share a divided mental scale.

The para-anoles (*Urostrophus** and *Anisolepis*) are not united by any apomorphies whose placement is independent of network, but para-anoles, *Polychrus*, and anoles may have a relationship supported in Topologies 1 and 2 (Fig. 11—Stem 2) by 39.1 (3 sternal ribs), 41.1 (loss of tail autotomy—reversed in anoles), and ambiguously by 34.3 (anole caudal vertebral type), which is difficult to evaluate in para-anoles (which are either "0" or "3") and *Polychrus* (either "2" or "3"). Alternatively, when oplurines or acrodonts are considered the sister-taxon of anoloids (Fig. 11—Stem 6), 36.2 (marginal and weak posterior coracoid fenestra), may support a special relationship of para-anoles with *Enyalius* + "*Pristidactylus*."

Enyalius is supported by 17.1 (far posterior extension of dentary [also seen in anoles]) and 64.1 (hemipenial accessory sheath muscle). In Topology 1 *Enyalius* is linked (Stem 3) with the anoles, para-anoles, and *Polychrus* by an elevated osseous labyrinth (13.1) (and possibly by a widened frontal); in Topology 2 and 3 *Enyalius* is linked (Stem 5) with "*Pristidactylus*" by 50.1 (divided terminal subdigital scales). Because the condition is unknown in para-anoles and *Enyalius*, all that can be said about the nasal condition (Transformation Series 56) is that either somewhere between "*Pristidactylus*" (56.0) and anoles + *Polychrus* (56.1), the nasal concha is lost, or, conversely, loss of the nasal concha may be a synapomorphy of *Polychrus* + anoles.

Anoloid monophyly is supported (Stem 4) in all networks and topologies by 14.1 (endolymphatic sacs penetrate nuchal musculature) and 61.2 (strongly bicapitate, bisulcate hemipenes). Some notable features of anoloids are ambiguously placed as apomorphies, either because of the possibility of greater levels of universality, or because of variability among anoloids: 7.1 (extensive skull rugosity—shared with chameleons and morunasaurs), and 40.1 (midventrally confluent postxiphisternal inscriptional ribs—shared with chameleons, morunasaurs, *Brachylophus*, and [in modified form] oplurines). In Topologies 1 and 2, 52.1 (spinulate scale organs) is considered an apomorphy for anoloids, but in Topology 3, this is regarded as a synapomorphy of anoloids + oplurines.

BASILISCINES

The topology of basiliscine relationships was stable in all networks and trees, and agrees with results presented by Etheridge and de Queiroz (1988) and Lang (1989), i.e., *Basiliscus* is the sister-taxon of *Corytophanes* + *Laemanctus*. Apomorphies of the group include: 10.2 (Y-shaped parietal roof with large median crest), 11.1 (parietal foramen in frontal [unknown in *Laemanctus*]), and 34.2 (basiliscine-type caudal vertebrae). In some topologies 63.1 (*m. retractor lateralis posterior* substantially in hemipenial sheath) falls on the ancestral stem, although it has a greater level of universality in other topologies. *Basiliscus* does not have apomorphies treated in this analysis whose placement is independent of network placement. In topologies where basiliscines are considered the sister-taxon of acrodonts, anoloids, or some combination, both superciliary and subocular scales in *Basiliscus* must return to the plesiomorphic condition (44.0 and 45.0), and in topologies where basiliscines are considered to be the sister-taxon of acrodonts, tail autotomy fracture planes (41.0) must be regained in *Basiliscus*. In our opinion, these hypothesized transformations reflect poorly on the likelihood of a special relationship of acrodonts and basiliscines, in light of the meager evidence supporting this relationship.

Corytophanes is well-corroborated by 13.1 (elevation of osseous labyrinth) and 31.1 (clavicle insertion of scapula). In some out-group topologies, 21.1 (shortened splenial) is also a feature of this stem. *Laemanctus* was specified in this analysis by development of extensive skull rugosity (7.1) and by secondary enlargement of the postfrontal (9.0), although placement of this character is ambiguous because *Basiliscus* and *Corytophanes* have reduced postfrontals (9.1). *Corytophanes* + *Laemanctus* monophyly is supported by 8.1 (broadly juxtaposed squamosal and jugal) and 10.3 (median parietal crest developed embryonically).

CROTAPHYTINES

The crotaphytines are remarkably plesiomorphic in many respects and lack any descriptively unique morphological features. Their monophyly is demonstrable only against the background of their out-groups, which possibly are either a group composed of sceloporines, oplurines, and tropidurines (and possibly including anoloids), or a group composed of acrodonts and basiliscines. With respect to these, the crotaphytines have arguably made three reversals: 27.0 (regain palatine teeth), 36.0 (regain posterior coracoid fenestrae), and 38.0 (develop ribs on the third cervical vertebra). More interestingly, the S-condition nasal apparatus (54.1) in the crotaphytines is only ambiguously considered homologous with that in the iguanines. *Crotaphytus* has only one unambiguous apomorphy in this analysis (7.1—extensive skull rugosity in older individuals) and *Gambelia* has none. It may well be that *Crotaphytus* and *Gambelia* are predatory relicts of a very old group.

IGUANINES

In no topology was there an unambiguous dichotomous resolution of the three iguanine taxa used in the analysis, although monophyly of the group is highly corroborated, both results in accordance with those of de Queiroz (1987) and Etheridge and de Queiroz (1988). Characters that support the monophyly of the iguanines in all topologies are: 12.1 (supratemporal mostly on the medial surface of the supratemporal process of the parietal), 34.1 (iguanine caudal vertebrae), and 65.1 (colic septa). Polycuspate teeth (25.1) and 54.1 (S-condition nasal apparatus) in some topologies have greater levels of universality. Unambiguous apomorphies of the three terminal taxa are: *Dipsosaurus*—11.1 (parietal foramen in frontal), *Brachylophus*—none, and iguanas—10.1 (V or Y-shaped parietal table). Our suspicion, however, is that *Dipsosaurus*, with its sceloporine-like superciliaries and suboculars, as well as unmodified postxiphisternal inscriptional ribs, is the sister-taxon of *Brachylophus* + other iguanines, which have broken-up suboculars, undifferentiated superciliaries and modified inscriptional ribs.

MORUNASAURS

The morunasaurs were initially presumed to be monophyletic (see "Choice of Terminal Taxa") on the basis of their very reduced vomers. No other apomorphies were discovered whose placement was independent of a particular network placement. In Networks A–B, F–G, I–L the morunasaurs were placed as the sister-taxon of the iguanines and in this topology three apomorphies obtained: 6.1 (lacrimal foramen enlarged), 7.1 (extensive skull rugosity), and 19.1 (anterior surangular foramen ventral to posterior extremity of dentary). In Network C (morunasaurs as the sister-taxon of iguanines) and in Network H (morunasaurs as the sister-taxon of anoloids + iguanines) only two characters are placed unambiguously on the morunasaur stem: 6.1 (enlarged lacrimal foramen) and 19.1 (anterior surangular foramen position). In Network D, the morunasaurs formed the sister-taxon of the anoloids and four unambiguously placed apomorphies obtained: 6.1 (lacrimal foramen enlarged), 18.0 (coronoid labial blade present), 19.1

(anterior surangular foramen position), and 25.1 (polycuspate marginal teeth). In Network E, morunasaurs are regarded as the sister-taxon of the acrodonts and the only unambiguously placed characters on the morunasaur stem are: 18.0 (regain coronoid labial blade) and 25.1 (polycuspate marginal teeth).

OPLURINES

In all topologies, the oplurines were supported as monophyletic by: 12.1 (supratemporal sits mostly on the medial surface of the supratemporal process of the parietal), 43.1 (interparietal black spot), and 58.1 (V-condition of ulnar nerve pathway). Other notable characteristics of oplurines, 40.2 (postxiphisternal inscriptional ribs forming paired splints) and 52.1 (spinulate scale organs) are only arguably synapomorphic or have greater levels of generality when oplurines and anoloids are considered sister-taxa (Fig. 7—Networks I–J); in other networks these features are unambiguously placed as apomorphies of the oplurines. *Oplurus* is supported as monophyletic by a reversal (39.0—four sternal ribs) and 38.2 (first pair of cervical ribs on vertebra 5); *Chalarodon* by 9.1 (postfrontal lost), 30.1 (clavicular flange reduced or absent), and a reversal (46.0—regaining of median enlarged dorsal scale row).

SCELOPORINES

Three, equally parsimonious sceloporine topologies were discovered that were independent of network (Fig. 12). In all three, monophyly of the sceloporines (Stem 1) was supported by: 28.1 (pterygoid teeth lost), 30.1 (clavicular flange reduced), 33.1 (posterior process of interclavicle invested by sternum anteriorly), 53.1 (sink-trap nasal apparatus), 60.1 (enlarged posterior lobe of hemipenis), and 62.1 (*m. retractor lateralis posterior* completely divided). Also common to all three topologies were: (1) *Uta* with no apomorphies; (2) *Petrosaurus* with two reversals, 38.0 (ribs on cervical vertebra 3) and 39.0 (4 sternal ribs); (3) *Phrynosoma* and the sand lizards (Stem 2) supported as monophyletic by 5.1 (lacrimal absent) and 9.1 (postfrontal absent).

Topology 1.—In the most common topology, Stem 3 (*Sceloporus*, *Urosaurus*, *Uta*, and *Petro-*

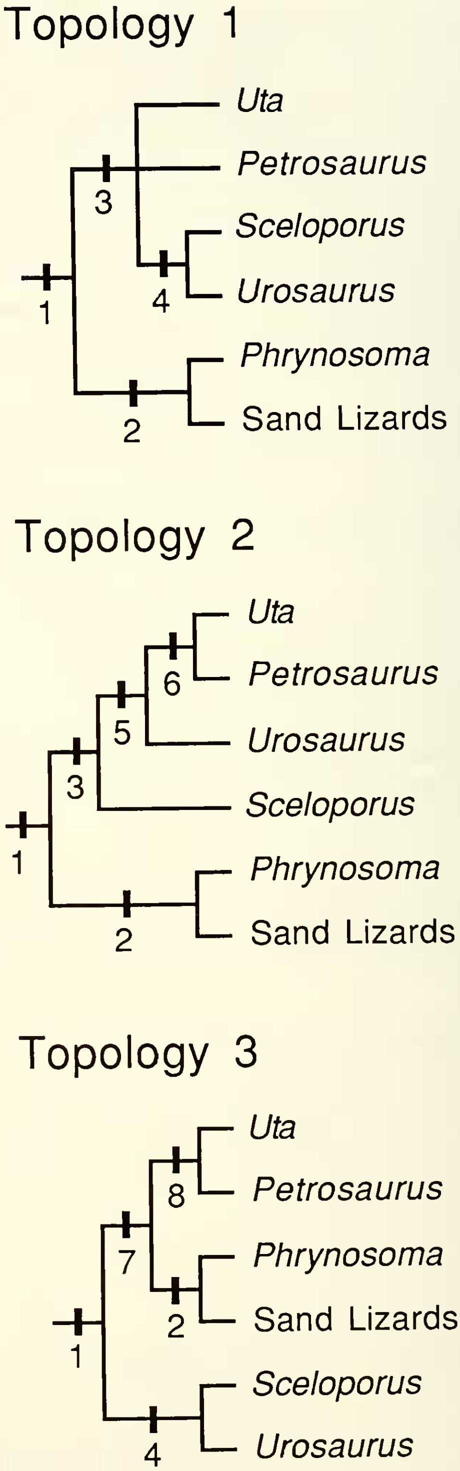

Fig. 12. Alternative topologies discovered within the sceloporines.

saurus) was supported by a greatly enlarged interparietal scale (42.1). This is ambiguous because if the small interparietal of *Uma* and *Phrynosoma* is secondary (and the large interparietal of *Callisaurus* and *Holbrookia* homologous), then this stem would be unsupported. However, a character of ambiguous placement, 35.1 (loss of scapular fenestra; reversed in *Sceloporus*), might support this stem. Also, taxa subtended by this stem have relatively well-developed frontal scales that, if independent of the interparietal scale development in this clade, would lend support to either this arrangement or Topology 2. Stem 4 (*Sceloporus* + *Urosaurus*) is supported by 59.1 (B-condition of shank innervation) and 66.1 (paired belly patches), the paired belly patches in sand lizards apparently being nonhomologous. However, the homologies of 66.1 are suspect, because "incipient" patches are seen in *Petrosaurus mearnsi* and the axillary spot of *Uta* may also be homologous. *Sceloporus* is supported by 47.1 (loss of gular fold) and a reversal, 35.0 (regaining scapular fenestra) and *Urosaurus* was supported by no apomorphies in this analysis. One character not included in this analysis because of among-group characterization problems, "hooked" clavicles (Etheridge, 1964) is congruent with this topology and would serve to place *Uta* as the sister-taxon of *Urosaurus* + *Sceloporus*.

Topology 2.—Stems 1–3 are as in Topology 1. *Sceloporus* is supported solely by 47.1 (loss of gular fold), but *Urosaurus* is linked (Stem 5) with *Uta* and *Petrosaurus*, rather than with *Sceloporus*, by 35.1 (loss of scapular fenestra). *Uta* and *Petrosaurus* are linked (Stem 6) by a reversal, 59.0 (A-condition of shank innervation).

Topology 3.—Stem 7 (*Phrynosoma*, sand lizards, *Petrosaurus*, and *Uta*) is supported by a reversal (59.0—A-condition of shank innervation) and *Uta* and *Petrosaurus* (Stem 8) are linked by 35.1 (loss of scapular fenestra), a feature shared convergently with *Urosaurus* in this topology.

Each of the three topologies is at variance with previously published cladograms (Presch, 1969; Etheridge and de Queiroz, 1988). In these earlier works, *Petrosaurus* was considered the sister-taxon of the remaining sceloporines, whereas we have no topologies in which this is the case. In earlier studies, absence of a nasal valve and four sternal ribs in *Petrosaurus* were considered plesiomorphic, but subsequently we concluded (following Malan, 1946) that erectile tissue surrounding the external naris is plesiomorphic for squamates. Also, presumptive near-relatives (e.g., "*Tropidurus*" west of the Andes) have nasal valves. Therefore, the lack of a nasal valve in *Petrosaurus* is only arguably plesiomorphic. The 4 sternal ribs of *Petrosaurus* are likely to be apomorphic when compared with the 3-sternal-ribbed tropidurines. Additionally, shimmy-burial, noted by Paull *et al.* (1976) and Etheridge and de Queiroz (1988) as a possible synapomorphy of the sceloporines, has been described in one species of "*Tropidurus*" (Dixon and Wright, 1975) and may be found in at least one species of "*Agama*" (Patterson, 1987). We suspect that this behavior could be simply plesiomorphic within Iguania.

TROPIDURINES

In this group, our results correspond reasonably closely to the results of Etheridge and de Queiroz (1988). In all networks (Fig. 7) the tropidurines (Fig. 13—Stem 1) are supported by two unambiguously placed features: 23.1 (reduced angular) and 47.1 (gular fold incomplete medially). In Network J, these features are joined by 22.1 (posterior extension of splenial) and in Network K by 37.1 (enlarged, median sternal fontanelle). Although this character list is not impressive, because these characters occur independently elsewhere in the tree, bear in mind that this resolution is not particularly sensitive to outgroup placement. Even if the oplurines are ex-

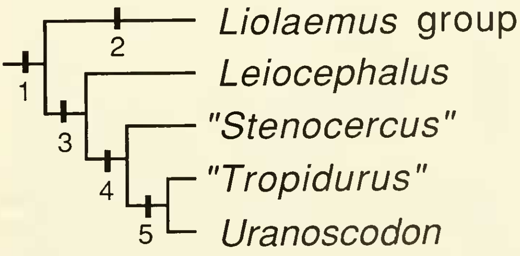

Fig. 13. Tropidurine topology.

cluded from the analysis (possibly the first outgroup of the tropidurines), this resolution still obtains. Stem 2 (Fig. 13—the *Liolaemus* group) is supported in all topologies by a reversal, 24.0 (posterior mylohyoid foramen anterior to level of apex of coronoid); and 35.1 (scapular fenestra absent), 49.1 (preanal pores present), and 54.1 (S-condition nasal apparatus). Alternative topologies exist in the *Liolaemus* group but this is discussed following the other tropidurines.

Stem 3, the "northern tropidurines" of Etheridge and de Queiroz (1988) are supported in all topologies by: 20.1 (fusion of Meckel's groove), 21.1 (splenial extends not more than 50% length of tooth row), and a reversal to 59.0 (B-condition of shank innervation). We regard the association of *Leiocephalus* with the "*Stenocercus*" and "*Tropidurus*" groups to be arguable. *Leiocephalus* shares with the *Liolaemus* group the premaxillary spine overlapped by the nasals (1.1—variable in *Phymaturus*) and an enlarged coronoid labial blade (8.0), which in this "neighborhood" of the cladogram is likely apomorphic. *Leiocephalus* is clearly monophyletic, supported by the characters mentioned in "Choice of Terminal Taxa" (10.1—shape of parietal roof; and 32.1—presence of an anterior process of the interclavicle).

Stem 4, supporting the monophyly of the "*Stenocercus*" + "*Tropidurus*" groups carries four unambiguously placed apomorphies: 24.2 (extreme posterior position of the posterior mylohyoid foramen), 36.0 (regaining of a posterior coracoid fenestra), 55.1 (fusion of the nasal concha to the roof of the nasal cavity [=reduction of the supraconchal cavity]), and 61.1 (bisulcate hemipenes). The "*Stenocercus*" group is weakly corroborated by 23.0 (secondary enlargement of the angular) and a feature noted in "Choice of Terminal Taxa," extensive hemipenial sheath musculature. Because of the poor resolution within the "*Stenocercus*" group, however, we regard its monophyly as not well documented.

Stem 5, the "*Tropidurus*" group ("*Tropidurus*" + *Uranoscodon*) is well-corroborated by four features: 33.1 (posterior process of the interclavicle invested by sternum far anteriorly), 42.1 (fused interparietal scales), 61.2 (strongly bicapitate hemipenes), and 64.1 (presence of a hemipenial dorsal accessory sheath muscle). No features analyzed support the monophyly of "*Tropidurus*" (but see "Choice of Terminal Taxa"), but the obviously highly apomorphic *Uranoscodon* has lost distinctive superciliaries and suboculars (44.1 and 45.1), regained a gular fold (47.0), and developed the B-condition of shank innervation (59.1).

TROPIDURINES: *LIOLAEMUS* GROUP

Within the tropidurines, the *Liolaemus* group has two topologies that are independent of network (Fig. 14). In both topologies, *Phymaturus* carries unambiguously three reversals: 21.0 (splenial extends anteriorly more than 50% length of tooth row), 38.0 (ribs on cervical vertebra 3), and 39.0 (sternal ribs 4 [although *Liolaemus* was coded "unknown" because it has 3 or 4]), plus 30.1 (clavicular flange reduced); and *Liolaemus* has a reversal (36.0—posterior coracoid fenestra present). In Topology 1, *Phymaturus* is the sister-taxon of *Ctenoblepharys* +

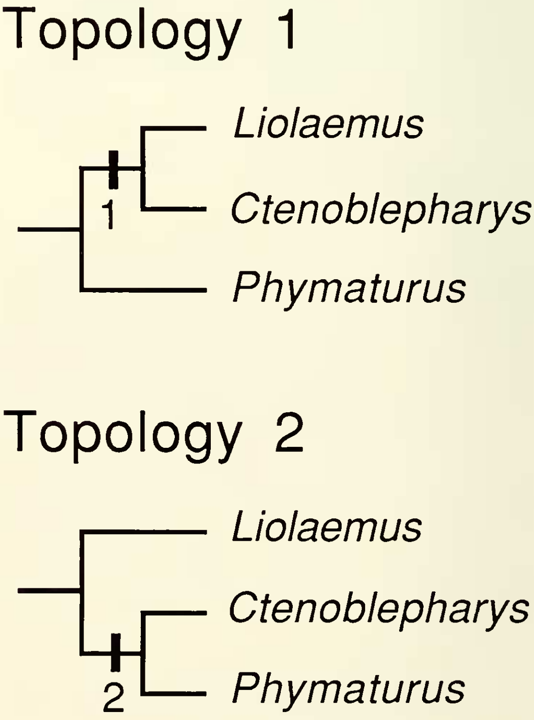

Fig. 14. Alternative topologies discovered within the *Liolaemus* group.

Liolaemus. Ctenoblepharys + *Liolaemus* (Stem 1) is supported by the supratemporal fitting in a groove on the supratemporal process of the parietal (12.2). In this topology *Ctenoblepharys* is apomorphic in character 45.1 (subocular divided), although *Phymaturus* was coded as "unknown" for this feature because of internal variability. In Topology 2, *Liolaemus* is the sister-taxon of *Ctenoblepharys* + *Phymaturus*, Stem 2, *Ctenoblepharys* + *Phymaturus* being supported by 45.1 (divided subocular). A feature noted by Arnold (1984) as possibly synapomorphic for the *Liolaemus* group, *m. retractor lateralis posterior* with a well-defined fleshy insertion, is also more well-developed in *Liolaemus* and *Ctenoblepharys* than in *Phymaturus*. Degree of development of this muscle supports Topology 1.

Although Topology 2 is analytically equal to Topology 1, it is important to note that it takes advantage of an "unknown" in *Phymaturus* (45.0 in *Phymaturus patagonicus*; 45.1 in *P. palluma*). Because *P. patagonicus* is otherwise more plesiomorphic than *P. palluma*, and because of the hemipenial musculature character of Arnold (1984) mentioned above we support Topology 1 as the most likely.

SCELOPORINES + OPLURINES + TROPIDURINES (+ ANOLOIDS)

In Networks A–H, and L (Fig. 7), sceloporines form the sister-taxon of oplurines + tropidurines (Fig. 15—Topology 1). In Network I, this arrangement is augmented by anoloids being placed as the sister-taxon of the oplurines (Fig. 15—Topology 2). In Network J, oplurines + anoloids form the sister-taxon of sceloporines + tropidurines (Fig. 15—Topology 3), and in Network K, the topology that obtains is sceloporines + (anoloids + [oplurines + tropidurines]) (Fig. 15—Topology 4). The "fence lizard" habitus of the sceloporines, tropidurines, and oplurines cannot be denied, and we think that this similarity is due to synapomorphy rather than homoplasy or plesiomorphy. The association of the anoloids with this group is more problematical, but worthy of serious consideration.

Topology 1.—Stem 1 (subtending the entire group) is corroborated by three characters that singly do not promote confidence against the backdrop of variability in Iguania: 39.1 (three sternal ribs [C.I.=*ca.* 0.16]) and 44.0 and 45.0, which are both reversals to likely plesiomorphic conditions of the superciliaries and enlarged suboculars. A fourth character (37.1), an enlarged sternal fontanelle, may support this clade, but condition 37.0 in oplurines makes placement of this feature ambiguous.

The monophyly of oplurines + tropidurines (Stem 2) is weakly supported by the widely homoplastic features 22.1 (splenial terminates posteriorly at the anterior edge of the mandibular fossa) and 48.1 (loss of femoral pores). Additionally, 17.1 (strong posterior extension of the dentary) may support this clade, but condition 17.0 in the *Liolaemus* group makes the character placement ambiguous.

Topology 2.—The subtending Stem 3 is roughly equivalent to Stem 1 of Topology 1, but with the addition of 21.1 (splenial extends anteriorly only ½ length of tooth row) to 39.1, 44.0, and 45.0 (discussed under "Topology 1"). Also in Stem 1 of Topology 1, 37.1 (enlarged sternal fontanelle) is placed ambiguously on this stem because of the absence of an enlarged fontanelle (37.0) in oplurines and anoloids. The monophyly of tropidurines + (oplurines + anoloids) (Stem 4) is supported by only one unambiguously placed character, 48.1 (loss of femoral pores), although 20.1 (fused Meckel's groove) and 22.1 (posterior position of posterior mylohyoid foramen) can be placed on this stem as one alternative.

The monophyly of anoloids + oplurines (Stem 5) is also supported by only one unambiguously placed character, 52.1 (spinulate scale organs). Assuming that the splint-like postxiphisternal inscriptional ribs (40.2) and the mid-ventrally continuous postxiphisternal inscriptional ribs (40.1) of anoloids are homologous at a more inclusive level than either is with 40.0 (nonelongate postxiphisternal inscriptional ribs) would add another unambiguous homologue on this stem and would serve to make this, or Topology 3, the preferred topology of the relationships between sceloporines, tropidurines, oplurines, and anoloids.

Character 37.0 (loss of an enlarged sternal fontanelle) is ambiguously considered a synapo-

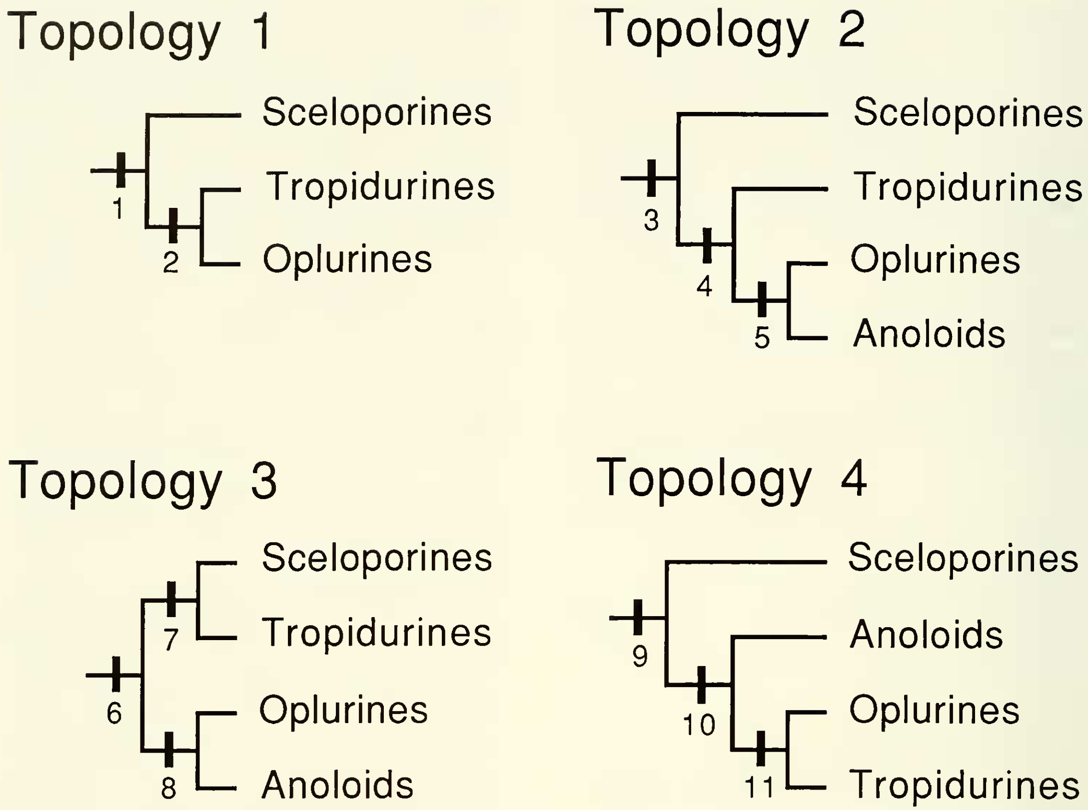

Fig. 15. Alternative topologies of sceloporines + oplurines + tropidurines (+ anoloids).

morphy of anoloids + oplurines in this topology because it depends on the enlarged median sternal fontanelle of sceloporines and tropidurines being a synapomorphy of the entire group (sceloporines, oplurines, tropidurines, and anoloids) with a reversal, rather than the independent acquisition of this feature in the sceloporine and tropidurine clades.

Topology 3.—Stem 6 is supported unambiguously by 21.1 (relatively short splenial), 39.1 (three sternal ribs), and 45.0 (subocular scale enlarged). Characters 44.0 (superciliaries elongate) and 48.1 (loss of femoral pores) are placed on the stem, although this arrangement would require sceloporines to develop femoral pores convergently.

The evidence supporting the monophyly of sceloporines + tropidurines (Stem 7) consists solely of one unambiguously placed character, 37.1 (single, enlarged median sternal fontanelle), although two other features can be placed on this stem under different character optimization, 44.1 (distinctly elongate superciliaries) and 59.1 (interosseus innervation of dorsal shank musculature).

Stem 8, subtending oplurines + anoloids, is also supported by a single unambiguously placed character, 52.1 (spinulate scale organs); although, as discussed under Stem 5 of Topology 2, assumption of homology between 40.1 (medially confluent postxiphisternal inscriptional ribs) and 40.2 (splint-like postxiphisternal inscriptional ribs) would add another character on this stem. Two other characters of ambiguous placement might also rest on this stem: 20.1 (fused Meckel's groove) and 48.1 (loss of femoral pores [which would require convergent loss in tropidurines]).

Topology 4.—Stem 9 (subtending the entire group) is corroborated by 21.1 (splenial extends ½ length of toothrow), 39.1 (three sternal ribs), and 45.0 (a reversal to having an enlarged subocular). Additionally, 44.0 (reversal to elongate superciliaries) may belong here, although this would require a change again to 44.1 in anoloids. Stem 10 (anoloids + [oplurines + tropidurines]) is supported by 48.1 (loss of femoral pores), although 20.1 (fused Meckel's groove) and 52.1 (spinulate scale organs [requiring a loss in tropidurines]) might be on this stem. Stem 11, uniting oplurines and tropidurines, is also supported by only one unambiguously placed character, 22.1 (posteriorly extended splenial), although this is convergent in anoles.

Although the evidence for a special relationship among the tropidurines, sceloporines, and oplurines is meager, alternatives, such as attempting to ally the Madagascan oplurines with the geographically proximate Afro-Australo-Asian acrodonts are considerably less parsimonious.

Summary of Results

Results of the analysis support the recognition of the suprageneric groups of Etheridge (1959, 1964, 1966, 1967) and Etheridge and de Queiroz (1988), as well as the acrodont group and its constituent parts. Our results do not support the hypothesized intragroup relationships of anoloids and sceloporines of Etheridge and de Queiroz (1988), the unambiguously supported monophyly of Agamidae* (Borsuk-Białynicka and Moody, 1984), nor the metataxon status of "Iguanidae" (because there is no evidence of monophyly in the face of incongruent evidence of paraphyly [Kluge, 1989]). No clear resolution of intergroup relationships within iguanids was obtained, although evidence of a relationship of the Madagascan oplurines with the American sceloporines and tropidurines (and possibly anoloids) was presented.

Although Schwenk (1988) was the first to present evidence that "Iguanidae" is paraphyletic with respect to Agamidae* + Chamaeleonidae, it appears from our analysis that his character evidence, presence of lingual reticular papillae (Char. 67.1), is homoplastic in anoles and acrodonts. For this feature to be synapomorphic would require either the paraphyly (or polyphyly) of the anoloids or the loss of the feature in anoloids other than anoles.

The results of our analysis show that continued recognition of Agamidae* and "Iguanidae" is not consistent with recovered historical relationships. Rather than maintain the unsupported collectives, Agamidae* and "Iguanidae," we propose to recognize as families, *sedis mutabilis* (Wiley, 1979, 1981a), the largest historical groups that are consistent with the strict consensus tree generated in the phylogenetic analysis of Iguania (Fig. 8). The taxonomy we have adopted (followed in parentheses by former taxonomic or informal equivalents) is listed below and also is illustrated in tree form in Figure 16.

Iguania Cope, 1864: *incertae sedis*: †*Aciprion** Cope, 1873; ?†*Arretosaurus** Gilmore, 1943; †*Carduciguana** Augé, 1987; †*Cypressaurus** Holman, 1972; ?†*Erichosaurus** Ameghino, 1899; ?†*Geiseltaliellus** Kuhn, 1944; †*Harrisonsaurus* Holman, 1981; †*Paradipsosaurus* Fries, Hibbard, and Dunkle, 1955; †*Parasauromalus* Gilmore, 1928; ?†*Pleurodontagama** Borsuk-Białynicka and Moody, 1984; †*Pristiguana** Estes and Price, 1973; ?†*Swain-*

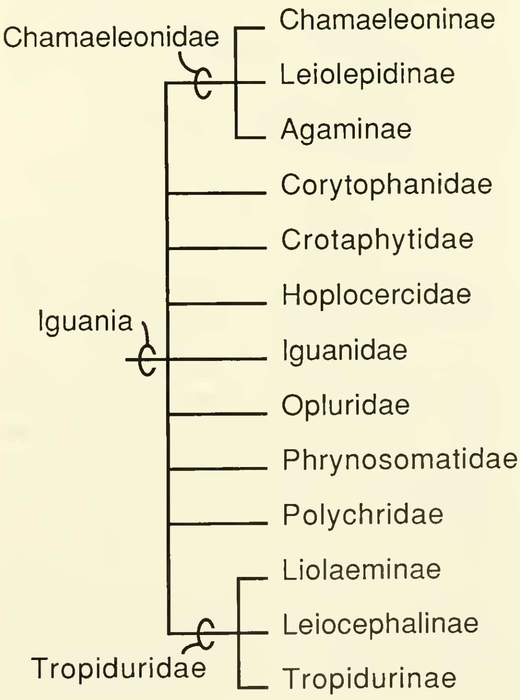

Fig. 16. Taxonomic tree.

*iguanoides** Sullivan, 1982.
Chamaeleonidae Rafinesque, 1815 (Acrodonta): *incertae sedis*: †*Mimeosaurus** Gilmore, 1943; †*Priscagama** Borsuk-Białynicka and Moody, 1984; †*Tinosaurus** Marsh, 1872.
  Agaminae Spix, 1825 (Agamidae*: Agaminae)
  Chamaeleoninae Rafinesque, 1815 (Chamaeleonidae)
  Leiolepidinae Fitzinger, 1843 (Agamidae*: Uromastycinae; or Uromastycidae)
Corytophanidae Fitzinger, 1843 ("Iguanidae": basiliscines)
Crotaphytidae Smith and Brodie, 1982 ("Iguanidae": crotaphytines)
Hoplocercidae new family ("Iguanidae": morunasaurs)
Iguanidae Oppel, 1811 ("Iguanidae": iguanines)
Opluridae Moody, 1983 ("Iguanidae": oplurines)
Phrynosomatidae Fitzinger, 1843 ("Iguanidae": sceloporines)
Polychridae Fitzinger, 1843 ("Iguanidae": anoloids)
Tropiduridae Bell, 1843 ("Iguanidae": tropidurines)
  Leiocephalinae new subfamily
  Liolaeminae new subfamily
  Tropidurinae Bell, 1843

The salient differences between this taxonomy and the traditional one (e.g., Camp, 1923; Estes *et al.*, 1988) are: (1) Agamidae* and Chamaeleonidae have been combined and (2) the informal groups within "Iguanidae" are accorded formal, independent taxonomic status. With the iguanid taxa this was unavoidable because these are the largest groups whose historical reality is well supported. Placing Agamidae* and Chamaeleonidae in one family was done because in this case we have considerable evidence that this is a single monophyletic group in a consensus polytomy with the former iguanid groups. We could have retained the name Acrodonta for this group, with three families within it (Chamaeleonidae, Leiolepididae [=Uromastycidae], and Agamidae). In doing so, however, we would not have been consistent in recognizing the largest monophyletic group of acrodonts as a family in symmetry with the other iguanian groups.

At this time we have chosen to recognize formal subfamilies only in the new, enlarged Chamaeleonidae (i.e., the former Acrodonta) and within Tropiduridae. We have taken this step in Chamaeleonidae because it is clear that not recognizing subfamilies would result in considerable confusion and because of the otherwise long-standing nomenclatural stability of its constituent groups. Within Tropiduridae we recognize subfamilies in order to simplify our other projects ongoing within these groups. Although de Queiroz (1987) proposed a suprageneric phylogenetic taxonomy within his Iguaninae (our Iguanidae), it was presented within a different philosophical context, so, rather than enter a philosophical discussion that is outside the scope of this paper we, without prejudice, do not address the subfamilial taxonomy of the iguanas.

In defense of our particular choice of rankings, we could have enlarged Iguanidae to include the acrodont and iguanid groups as subfamilies (i.e., made Iguanidae equivalent to Iguania). This would have rendered an enlarged Iguanidae coextensive (=redundant) with Iguania. However, by using the Linnaean family-group category as we have, we advertise the lack of intergroup resolution, while avoiding nomenclatural redundancy. We recognize, of course, that ranking is arbitrary and we see "families" not as members of some natural class of comparable entities, but as merely nomenclaturally internally consistent "files" in the Linnaean book-keeping system used throughout biology.

We realize that the new taxonomy and nomenclature will not be popular with those preferring a classification rooted in social tradition or in some arbitrary measure of overall similarity. And, if Agamidae were an older name than Chamaeleonidae, we doubt that there would be much controversy regarding that nomenclatural change, because systematics as practiced by the majority of workers has little to do with evolution and much to do with a crude sort of essentialism.

TAXONOMIC ACCOUNTS AND CHARACTERIZATIONS

The characterizations provided for the families and subfamilies are not lists of apomorphies; those data are available in Appendices 2 and 3 and in "Results." The characterizations allow the taxa to be differentiated from the other taxa of equal rank in this section. Metataxon and quotation conventions are suspended in synonymies for nomenclatural clarity.

IGUANIA COPE, 1864

1864. Iguania Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:226.

Characterization.—(1) frontals fused embryonically (Jollie, 1960; Estes *et al.*, 1988); (2) frontals constricted between the orbits (reversed in some groups) (Estes *et al.*, 1988); (3) broad frontal shelf underlying nasals (Estes *et al.*, 1988); (4) postfrontal reduced (Estes *et al.*, 1988; Presch, 1988); (5) dracomorph brain-stem morphology (Northcutt, 1978); (6) *m. intercostalis ventralis* absent (Camp, 1923); (7) tongue mucocytes mostly serous and sero-mucous (Gabe and Saint Girons, 1969; Schwenk, 1988).

Content.—Those taxa that together form the sister-taxon of Scleroglossa (=Scincogekkonomorpha); traditional "Iguanidae," Agamidae*, and Chamaeleonidae; here recognized as Chamaeleonidae (including former Uromastycidae and Agamidae*), Corytophanidae, Crotaphytidae, Hoplocercidae, Iguanidae, Opluridae, Phrynosomatidae, Polychridae, and Tropiduridae.

Distribution.—All continental temperate and tropical regions. Absent from most of Oceania.

Comment.—The attribution of the name Iguania to Cuvier (1817) is in error; Cuvier used the explicit (though non-Latinized) family-group name Iguaniens. The first author to use the name Iguania was Cope (1864), the same author that coined the name Acrodonta for a group composed of the former Agamidae* and Chamaeleonidae (in the old sense), now equivalent to Chamaeleonidae.

CHAMAELEONIDAE RAFINESQUE, 1815

1815. Camelonia Rafinesque, Analyse Nat.:75. Type genus: "*Camaeleo* Daud." (=*Chamaeleo* Daudin, 1802 =*Chamaeleo* Laurenti, 1768).

1825. Agamae Spix, Anim. Nov. Spec. Nova Lacert.:12. Type genus: *Agama* Daudin, 1802.

1825. Camelionidae Gray, Ann. Philos., (2)10:200. Type genus: "*Chamelion*, Lin." (=*Chamelion* Gray, 1825, a likely incorrect subsequent usage of *Chamaeleon* Gronovius, 1763, a rejected name [Opinion 89]).

1825. Stellionidae Bell, Zool. J., London, 2:457. Type genus: "*Stellio* Daudin" (not *Stellio* Laurenti, 1768). See Stejneger *in* Smith (1932) and Smith (1957) for discussion.

1826. Draconoidea Fitzinger, Neue Classif. Rept.:11. Type genus: "*Draco* Kaup" (=*Draco* Linnaeus, 1758).

1843. Gonyocephali Fitzinger, Syst. Rept., 1:15. Type genus: "*Gonyocephalus* Kaup (Cuv.)" (=*Gonocephalus* Kaup, 1825).

1843. Calotae Fitzinger, Syst. Rept., 1:15. Type genus: "*Calotes* Kaup" (=*Calotes* Cuvier, 1817).

1843. Semiophori Fitzinger, Syst. Rept., 1:15. Type genus: "*Semiophorus* Wagl[er]." (=*Sitana* Cuvier, 1829).

1843. Otocryptae Fitzinger, Syst. Rept., 1:15. Type genus: "*Otocryptis* Wiegm[ann]." (=*Otocryptis* Wagler, 1830).

1843. Lophurae Fitzinger, Syst. Rept., 1:15. Type genus: "*Lophura* Wagl[er]. (Gray)" (=*Lophura* Gray, 1827 =*Hydrosaurus* Kaup, 1828).

1843. Trapeli Fitzinger, Syst. Rept., 1:17. Type genus: *Trapelus* Cuvier, 1817.

1843. Phrynocephali Fitzinger, Syst. Rept., 1:18. Type genus: *Phrynocephalus* Kaup, 1825.

1923. Brookesinae Nopsca, Fortschr. Geol. Palaeont., 2:124. Type genus: *Brookesia* Gray, 1865.

1984. Priscagaminae Borsuk-Białynicka and Moody, Acta Palaeontol. Polon., 29:54. Type genus: *Priscagama* Borsuk-Białynicka and Moody, 1984. See comment.

Characterization.—(1) maxillae meet broadly anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen variably enlarged; (3) skull roof variably rugose (only chameleons and †*Priscagama**); (4) jugal and squamosal broadly juxtaposed (not †*Priscagama**); (5) parietal roof shape quadrangular (or domed in chameleons); (6) parietal foramen usually absent, if present, on frontoparietal suture; (7) supratemporal on lateral side of supratemporal process of parietal, except in chameleons in which its reduced to a small splint on the medioocaudal edge of the ventral ramus of the squamosal and has lost entirely any connection of the parietal (Rieppel, 1981); (8) nuchal endolymphatic sacs penetrating nuchal musculature only in some *Brookesia* (Chamaeleoninae); (9) dentary expanded onto labial face of coronoid (except †*Priscagama**); (10) no labial blade of coronoid; (11) anterior surangular foramen inferior to posteriormost extent of dentary; (12) Meckel's groove broadly open; (13) splenial short anteriorly, or absent; (14) dentary and maxillary teeth acrodont, fused to underlying bone in adults; (15) palatine teeth absent (present in †*Priscagama**); (16) pterygoid teeth absent (present in †*Priscagama**); (17) posterior process of interclavicle not invested by sternum far anteriorly; (18) no caudal autotomy (except some *Uromastyx*), caudal vertebrae with single transverse processes anteriorly; (19) posterior coracoid fenestra absent, except in *Uromastyx*; (20) sternal fontanelles present or absent; (21) number of sternal ribs variable; (22) postxiphisternal inscriptional ribs variable; (23) interparietal scale not enlarged; (24) mid-dorsal scale row variable; (25) gular fold complete medially, except chameleons; (26) femoral pores present or absent; (27) spinulate scale organs absent (except in some chameleons; the spiked scale organs of some agamines are clearly not homologous); (28) acrodontan nasal apparatus (except *Physignathus*), vestibule long, concha reduced or absent; (29) hemipenes variable, none known to be bicapitate or bisulcate; (30) colic septa absent (except in *Uromastyx* and *Hydrosaurus*).

Content.—Agaminae Spix, 1825; Chamaeleoninae Rafinesque, 1815; and Leiolepidinae Fitzinger, 1843.

Distribution.—Tropical and temperate regions of Africa, Madagascar, southern Europe, Asia, and Australia (Fig. 17).

Comment.—As here used, Chamaeleonidae is equivalent to Acrodonta of Estes *et al.* (1988). Former Agamidae* and Chamaeleonidae are synonymized because the monophyly of Agamidae* is only ambiguously supported (Camp, 1923; Estes *et al.*, 1988; *contra* Borsuk-Białynicka and Moody, 1984), even though the traditional Chamaeleonidae (the chameleons) is well supported. The constituent taxa of †Priscagaminae* Borsuk-Białynicka and Moody (1984) are relegated to the status of *incertae sedis* within the Chamaeleonidae because they are not tied together unambiguously by apomorphies, although they are clearly plesiomorphic with respect to any of the named suprageneric taxa within the Chamaeleonidae.

AGAMINAE SPIX, 1825

1825. Agamae Spix, Anim. Nov. Spec. Nova Lacert.:12. Type genus: *Agama* Daudin, 1802.

1825. Stellionidae Bell, Zool. J., London, 2:457. Type genus: "*Stellio* Daudin" (not *Stellio* Laurenti, 1768). See Stejneger *in* Smith (1932) for discussion of unavailability of *Stellio* for any member of Iguania.

1826. Draconoidea Fitzinger, Neue Classif. Rept.:11. Type genus: "*Draco* Kaup" (=*Draco* Linnaeus, 1758).

1843. Gonyocephali Fitzinger, Syst. Rept., 1:15. Type genus: "*Gonyocephalus* Kaup (Cuv.)" (=*Gonocephalus* Kaup, 1825).

1843. Calotae Fitzinger, Syst. Rept., 1:15. Type genus: "*Calotes* Kaup" (=*Calotes* Cuvier, 1817).

1843. Semiophori Fitzinger, Syst. Rept., 1:15. Type genus: "*Semiophorus* Wagl[er]." (=*Sitana* Cuvier, 1829).

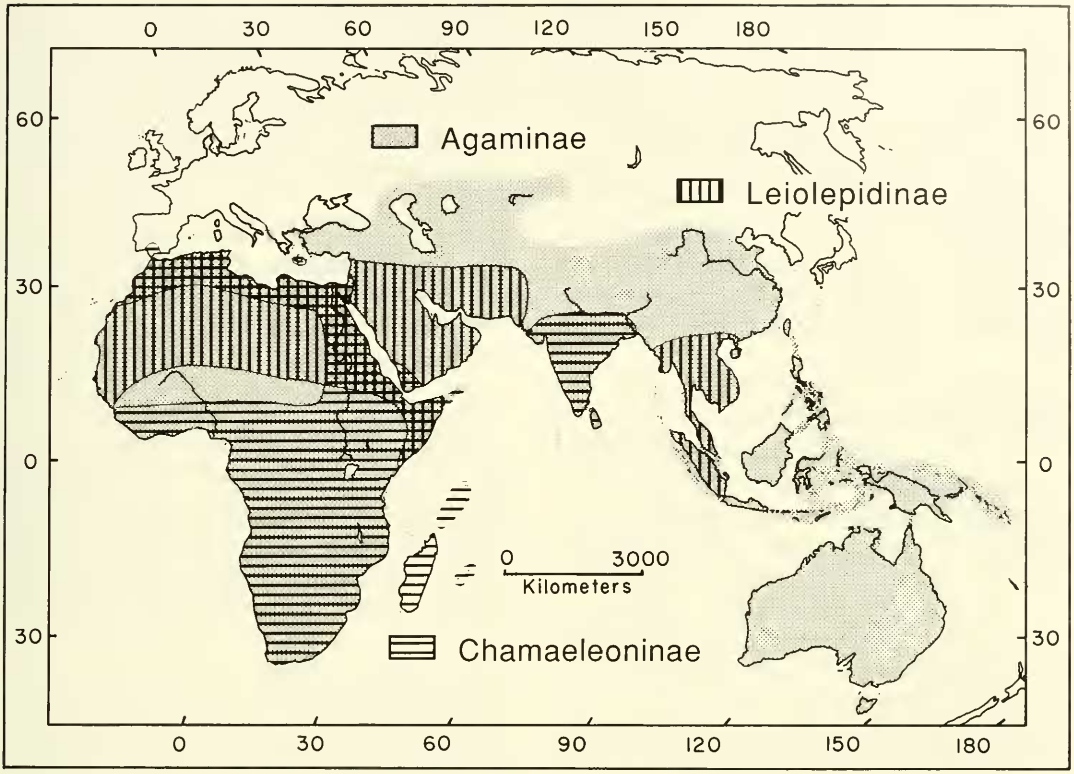

Fig. 17. Distribution of Chamaeleonidae, including subfamilies.

1843. Otocryptae Fitzinger, Syst. Rept., 1:15. Type genus: "*Otocryptis* Wiegm[ann]." (=*Otocryptis* Wagler, 1830).

1843. Lophurae Fitzinger, Syst. Rept., 1:15. Type genus: "*Lophura* Wagl[er]. (Gray)" (=*Lophura* Gray, 1827 =*Hydrosaurus* Kaup, 1828).

1843. Trapeli Fitzinger, Syst. Rept., 1:17. Type genus: *Trapelus* Cuvier, 1817.

1843. Phrynocephali Fitzinger, Syst. Rept., 1:18. Type genus: *Phrynocephalus* Kaup, 1825.

Characterization.—(1) vomer flat or convex; (2) lacrimal foramen extremely enlarged; (3) skull roof not rugose or domed; (4) epiotic foramen present (except in *Moloch*); (5) interclavicle present; (6) paired, enlarged sternal fontanelles; (7) postxiphisternal inscriptional ribs short; (8) femoral pores present plesiomorphically; (9) normal feet.

Content[6].—*Acanthosaura* Gray, 1831; "*Agama*" Daudin, 1802; "*Amphibolurus*" Wagler, 1830; *Aphaniotis* Peters, 1864; *Caimanops* Storr, 1974; "*Calotes*" Cuvier, 1817; *Ceratophora* Gray, 1834; *Chelosania* Gray, 1845; *Clamydosaurus*[7] Gray, 1825; *Cophotis* Peters, 1861; *Cryptagama* Witten, 1984; *Dendragama* Doria, 1888; *Diporiphora** Gray, 1842; *Draco* Linnaeus, 1758; "*Gonocephalus*" Kaup, 1825; *Harpesaurus* Boulenger, 1885; *Hydrosaurus* Kaup, 1828; *Hylagama* Mertens, 1924; *Japalura* Gray, 1853; *Lophocalotes* Günther, 1872; *Lophognathus* Gray, 1842; *Lyriocephalus* Merrem, 1820; *Mictopholis* Smith, 1935; *Moloch* Gray, 1841; *Oriocalotes* Günther, 1864; *Otocryptis* Wagler, 1830; *Phoxophrys* Hubrecht,

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[6] Until the controversy surrounding the nomenclatural validity of names proposed by Wells and Wellington (1983) is resolved, we refrain from using their names.

[7] Usually unjustifiably emended to *Chlamydosaurus.*

1881; *Phrynocephalus* Kaup, 1825; *Physignathus* Cuvier, 1829; *Psammophilus* Fitzinger, 1843; *Ptyctolaemus* Peters, 1864; *Salea* Gray, 1845; *Sitana* Cuvier, 1829; "*Tympanocryptis*" Peters, 1863; *Xenagama* Boulenger, 1895.

Distribution.—Temperate and tropical Eurasia, Africa, and Australia, including associated islands (Fig. 17).

Comment.—As here used, Agaminae is equivalent to Agamidae of previous authors, but excluding *Uromastyx* and *Leiolepis*.

CHAMAELEONINAE RAFINESQUE, 1815

1815. Camelonia Rafinesque, Analyse Nat.:75. Type genus: "*Camaeleo* Daud." (=*Chamaeleo* Daudin, 1802 =*Chamaeleo* Laurenti, 1768).

1825. Camelionidae Gray, Ann. Philos., (2)10:200. Type genus: "*Chamelion*, Lin." (=*Chamelion* Gray, 1825, a likely incorrect subsequent usage of *Chamaeleon* Gronovius, 1763, a rejected name (Opinion 89).

1923. Brookesinae Nopsca, Fortschr. Geol. Palaeont., 2:124. Type genus: *Brookesia* Gray, 1865. See comment.

Characterization.—(1) vomer flat or convex; (2) lacrimal foramen extremely enlarged; (3) skull roof domed and rugose; (4) epiotic foramen absent; (5) interclavicle absent; (6) no sternal fontanelles; (7) postxiphisternal inscriptional ribs elongate, fused medially; (8) femoral pores absent; (9) zygodactyl feet.

Content.—*Brookesia* Gray, 1865; *Calumma** Gray, 1864; *Chamaeleo* Laurenti, 1768; *Bradypodion* Fitzinger, 1843; *Furcifer* Fitzinger, 1843; *Rhampholeon* Günther, 1874.

Distribution.—Extreme southwestern Europe, Africa (excluding the Sahara), southwestern and northwestern Arabia, Madagascar, Seychelles, India, and Sri Lanka, and associated islands (Fig. 17).

Comment.—Our purpose here is not to evaluate previous work on the phylogeny of chameleons, and although we have Brookesiinae Nopsca (Klaver and Böhme, 1986) in the synonymy of Chamaeleonidae, this is only in recognition of Brookesiinae as a family-group name. Because our Chamaeleoninae is the equivalent of Chamaeleonidae of previous authors, we simply regard Brookesiinae and Chamaeleoninae of Klaver and Böhme (1986) to be tribes, Brookesiini (containing *Brookesia* and *Rhampholeon*) and Chamaeleonini (containing *Calumma**, *Furcifer, Bradypodion*, and *Chamaeleo*).

LEIOLEPIDINAE FITZINGER, 1843

1843. Leiolepides Fitzinger, Syst. Rept., 1:18. Type genus: *Leiolepis* Cuvier, 1829.

1868. Uromasticidae Theobald, J. Linn. Soc. Zool., 10:34. Type genus: *Uromastix* Merrem, 1820 (=*Uromastyx* Merrem, 1820).

Characterization.—(1) vomer concave; (2) lacrimal foramen not enlarged; (3) skull roof not rugose or domed; (4) epiotic foramen absent; (5) interclavicle present; (6) paired, enlarged sternal fontanelles; (7) postxiphisternal inscriptional ribs short; (8) femoral pores present; (9) normal feet.

Content.—*Leiolepis* Cuvier, 1829; *Uromastyx* Merrem, 1820.

Distribution.—Deserts of North and East Africa and Arabia to Iran, Afghanistan, Pakistan, and western India; southern India and southern China through Indochina to Sumatra (Fig. 17).

Comment.—Although this taxon has been recognized previously (e.g., Borsuk-Białynicka and Moody, 1984), the name of priority is Leiolepidinae rather than Uromastycinae.

CORYTOPHANIDAE FITZINGER, 1843

1843. Corythophanae Fitzinger, Syst. Rept., 1:16. Type genus: "*Corythophanes* Boie" (=*Corytophanes* Boie, 1827).

1900. Basiliscinae Cope, Annu. Rept. U.S. Natl. Mus. for 1899:223. Type genus: *Basiliscus* Laurenti, 1768.

Characterization.—(1) maxillae not meeting anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen not enlarged; (3) skull roof not strongly rugose (except in *Laemanctus*); (4) jugal and squamosal broadly juxtaposed in *Corytophanes* and *Laemanctus*; (5) parietal roof Y-shaped with median crest formed postembryonically in *Basiliscus*, embryonically in *Laemanctus* and *Corytophanes*; (6) parietal foramen in frontal (parietal foramen absent in *Laemanctus*); (7) supratemporal sits on lateral side of supratemporal process of parietal; (8) nuchal endolymphatic sacs not penetrating nuchal musculature; (9) dentary not expanded onto labial face of coronoid; (10) no labial blade of coronoid; (11) anterior surangular foramen superior to posteriormost extent of dentary; (12) Meckel's groove fused (except in some *Basiliscus*); (13) splenial relatively short (*Corytophanes*) or long (*Basiliscus* and *Laemanctus*) anteriorly; (14) dentary and maxillary teeth pleurodont, not fused to underlying bone in adults; (15) palatine teeth absent; (16) pterygoid teeth present; (17) posterior process of interclavicle not invested by sternum far anteriorly; (18) caudal autotomy fracture planes present (except *Laemanctus*), with transverse processes weak or absent; (19) posterior coracoid fenestra absent; (20) sternal fontanelles very small or absent; (21) sternal ribs 4; (22) postxiphisternal inscriptional ribs short; (23) interparietal scale not enlarged; (24) median dorsal scale row enlarged; (25) gular fold complete medially; (26) femoral pores absent; (27) spinulate scale organs absent; (28) nasal apparatus primitive, nasal vestibule short, simple; concha present, free; (29) hemipenes unicapitate, unisulcate; (30) colic septa absent.

Content.—*Basiliscus* Laurenti, 1768; *Corytophanes* Boie, 1827; *Laemanctus* Wiegmann, 1834.

Distribution.—Western and eastern Mexico, southward through Central America, to Ecuador and Venezuela (Fig. 18).

Comment.—This family corresponds to the "basiliscines" of Etheridge *in* Paull *et al.* (1976), Etheridge and de Queiroz (1988), and Lang (1989).

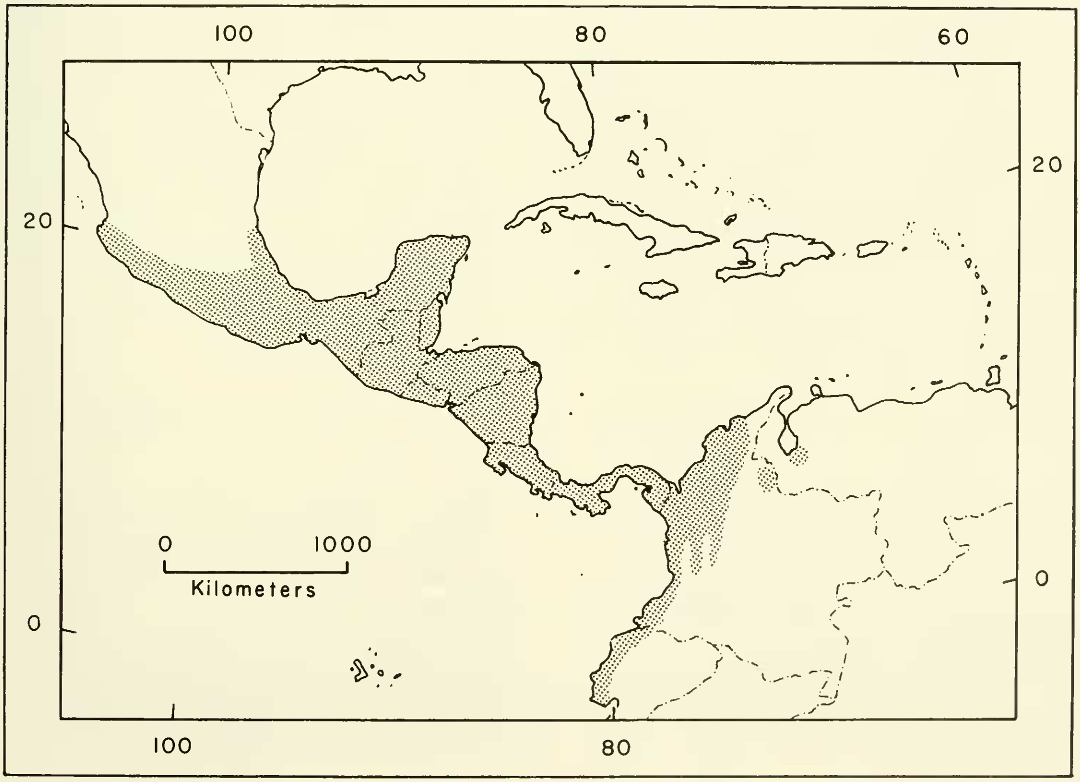

Fig. 18. Distribution of Corytophanidae.

CROTAPHYTIDAE SMITH AND BRODIE, 1982

1982. Crotaphytinae Smith and Brodie, Guide Field Ident. Reptiles N. Am.:106. Type genus: *Crotaphytus* Holbrook, 1842.

Characterization.—(1) maxillae not meeting anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen not enlarged; (3) skull roof not strongly rugose, except in old *Crotaphytus*; (4) jugal and squamosal not broadly juxtaposed; (5) parietal roof trapezoidal; (6) parietal foramen in frontoparietal suture; (7) supratemporal sits on lateral side of supratemporal process of parietal; (8) nuchal endolymphatic sacs do not penetrate nuchal musculature; (9) dentary not expanded onto labial face of coronoid; (10) labial blade of coronoid poorly developed or absent; (11) anterior surangular foramen above posteriormost extent of dentary; (12) Meckel's groove not fused; (13) splenial relatively long anteriorly; (14) dentary and maxillary teeth pleurodont, not fused to underlying bone in adults; (15) palatine teeth present; (16) pterygoid teeth present; (17) posterior process of interclavicle not invested by sternum far anteriorly; (18) caudal autotomy fracture planes present (except in *Crotaphytus*), with transverse processes anterior to fracture planes; (19) posterior coracoid fenestra present; (20) sternal fontanelles very small or absent; (21) sternal ribs 4; (22) postxiphisternal inscriptional ribs short; (23) interparietal scale not enlarged; (24) mid-dorsal scale row absent; (25) gular fold complete medially; (26) femoral pores present; (27) spinulate scale organs absent; (28) S-condition nasal apparatus; nasal vestibule long, S-shaped, concha present; (29) hemipenes unicapitate, unisulcate; (30) colic septa absent.

Content.—*Crotaphytus* Holbrook, 1842; *Gambelia* Baird and Girard, 1859.

Distribution.—Southwestern North America from eastern Oregon to the Mississippi River and south to northern Mexico (Fig. 19).

Comment.—Crotaphytidae corresponds to the "crotaphytines" of Etheridge and de Queiroz (1988).

HOPLOCERCIDAE NEW FAMILY

Type genus.—*Hoplocercus* Fitzinger, 1843.

Characterization.—(1) maxillae not meeting anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen enlarged; (3) skull roof strongly rugose (except in *Hoplocercus* and "*Morunasaurus*"); (4) jugal and squamosal not broadly juxtaposed; (5) parietal roof trapezoidal; (6) parietal foramen in frontoparietal suture (absent in some "*Morunasaurus*"); (7) supratemporal sitting on lateral side of supratemporal process of parietal; (8) nuchal endolymphatic sacs not penetrating nuchal musculature; (9) dentary not expanded onto labial face of coronoid; (10) labial blade of coronoid large; (11) anterior surangular foramen inferior to posteriormost extent of dentary; (12) Meckel's groove not fused; (13) splenial very large, penetrating far anteriorly; (14) dentary and maxillary teeth pleurodont, not fused to underlying bone in adults; (15) palatine teeth absent; (16) pterygoid teeth present; (17) posterior process of interclavicle not invested by sternum far anteriorly; (18) caudal autotomy fracture planes present (except *Hoplocercus*), with transverse processes anterior to fracture planes; (19) posterior coracoid fenestra absent (except in "*Morunasaurus*" *annularis*); (20) sternal fontanelles very small or absent; (21) sternal ribs number 4; (22) postxiphisternal inscriptional ribs long, confluent medially; (23) interparietal scale not enlarged; (24) mid-dorsal scale row present (except in "*Morunasaurus*" and *Hoplocercus*); (25) gular fold complete medially; (26) femoral pores present; (27) spinulate scale organs absent; (28) primitive nasal apparatus; nasal vestibule short, straight; concha present, free; (29) hemipenes unicapitate, unisulcate; (30) colic septa absent.

Content.—"*Enyalioides*" Boulenger, 1885; *Hoplocercus* Fitzinger, 1843; "*Morunasaurus*" Dunn, 1933.

Distribution.—Eastern Panama to the Pacific lowlands of Ecuador; Upper Amazonian Basin of Brazil, Colombia, Ecuador, and Peru; southeastern Brazil (Fig. 20).

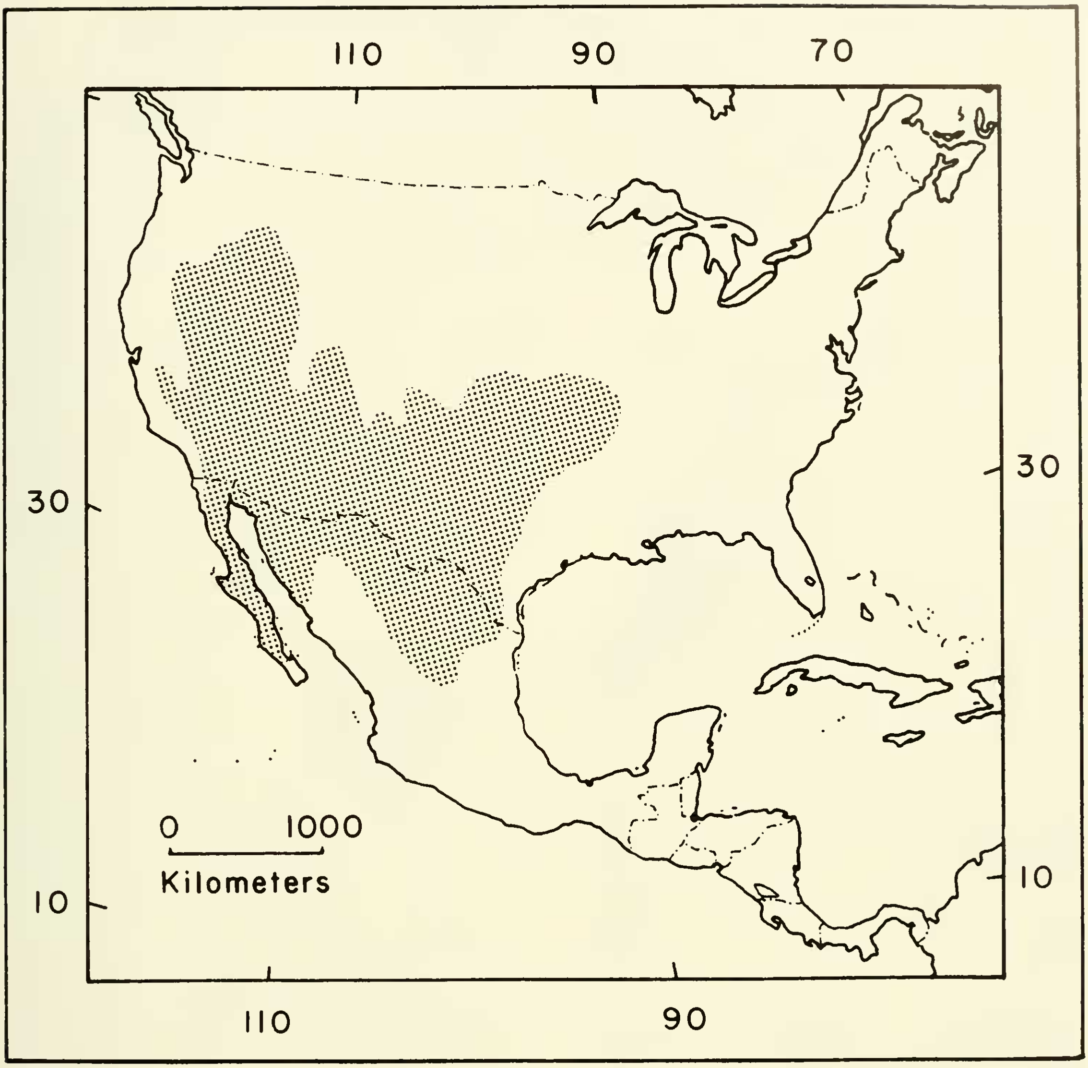

Fig. 19. Distribution of Crotaphytidae.

Comment.—Hoplocercidae corresponds to the "hoplocercines" of Smith *et al.* (1973), "morunasaurines" of Estes and Price (1973), and the "morunasaurs" of Etheridge and de Queiroz (1988). We have employed *Hoplocercus* as the type genus, rather than "*Morunasaurus*," because *Hoplocercus* is the oldest generic name in the clade and the only name that does not refer currently to a paraphyletic grouping (Etheridge and de Queiroz, 1988).

IGUANIDAE OPPEL, 1811

1811. Iguanoides Oppel, Ordn. Fam. Gatt. Rept.:26. Type genus: "*Iguana* Linné" (=*Iguana* Laurenti, 1768).

1843. Hypsilophi Fitzinger, Syst. Rept., 1:16. Type genus: *Hypsilophus* Wagler, 1830 (=*Iguana* Laurenti, 1768).

1987. Amblyrhynchina de Queiroz, Univ. California Publ. Zool., 118:160. Type

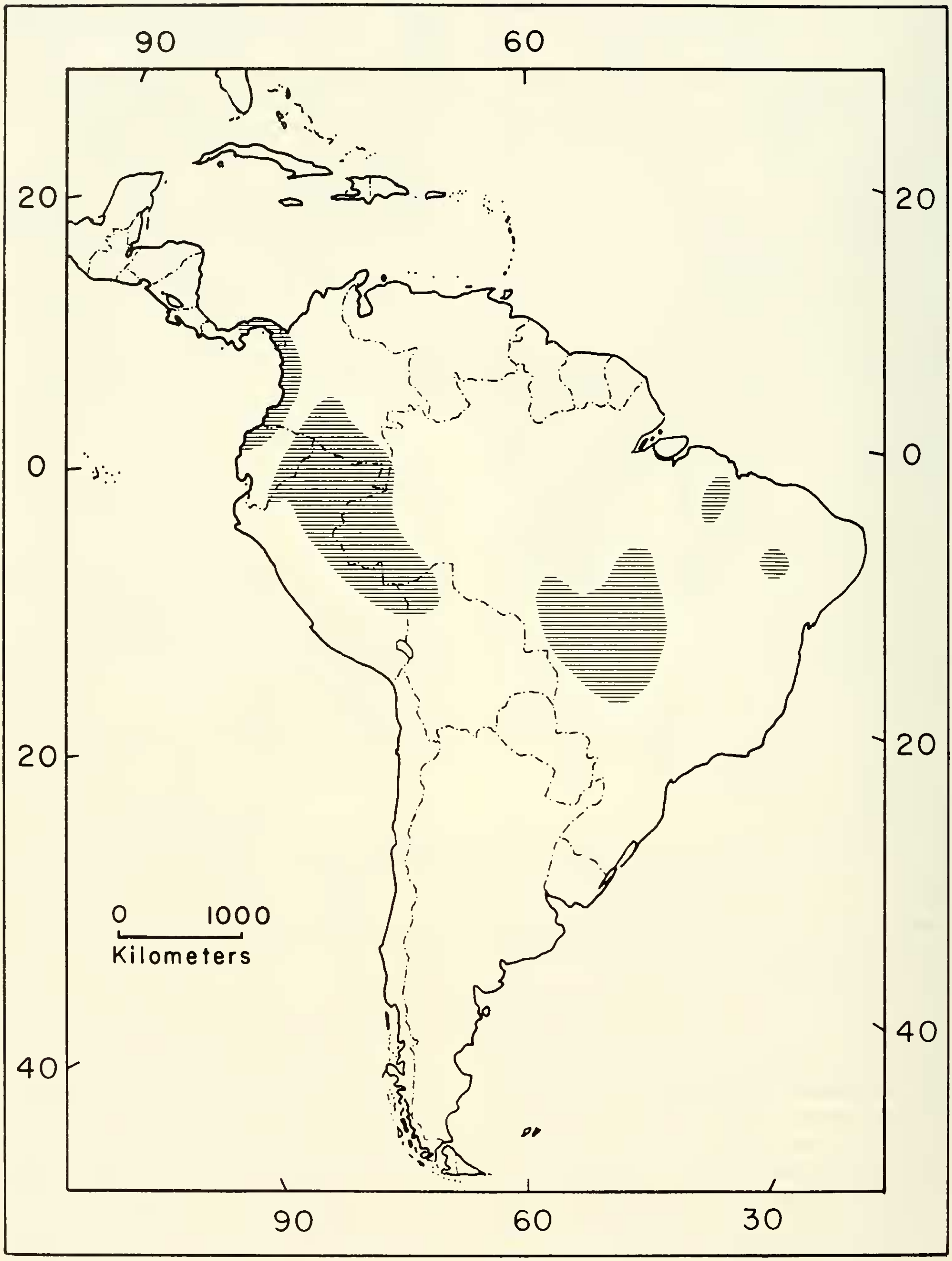

Fig. 20. Distribution of Hoplocercidae.

genus: *Amblyrhynchus* Bell, 1825. See comment.

Characterization.—(1) maxillae not meeting anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen not enlarged; (3) skull roof not strongly rugose (except *Amblyrhynchus*); (4) jugal and squamosal not broadly juxtaposed; (5) parietal roof variable; (6) parietal foramen in frontoparietal suture (in frontal in *Dipsosaurus*); (7) supratemporal sits on medial side of supratemporal process of parietal; (8) nuchal endolymphatic sacs not penetrating nuchal musculature; (9) dentary not expanded onto labial face of coronoid; (10) labial blade of coronoid large; (11) anterior surangular foramen superior to posteriormost extent of dentary; (12) Meckel's groove fused; (13) splenial relatively short anteriorly; (14) dentary and maxillary teeth pleurodont, not fused to underlying bone in adults; (15) palatine teeth absent; (16) pterygoid teeth present; (17) posterior process of interclavicle not invested by sternum far anteriorly; (18) caudal autotomy fracture planes present (except in *Amblyrhynchus, Conolophus, Brachylophus,* and *Iguana delicatissima*), with transverse processes anterior and posterior to fracture planes (when present) of anterior autotomic vertebrae; (19) posterior coracoid fenestra present; (20) sternal fontanelles very small or absent; (21) sternal ribs 4; (22) postxiphisternal inscriptional ribs variable (long and confluent medially in some); (23) interparietal scale not enlarged; (24) mid-dorsal scale row present (absent in *Sauromalus* and some *Ctenosaura*); (25) gular fold complete medially; (26) femoral pores present; (27) spinulate scale organs absent; (28) S-condition nasal apparatus; nasal vestibule long, S-shaped; concha present (29) hemipenes unicapitate, unisulcate; (30) colic septa present.

Content.—*Amblyrhynchus* Bell, 1825; *Brachylophus* Cuvier, 1829; *Conolophus* Fitzinger, 1843; *Ctenosaura* Wiegmann, 1828; *Cyclura* Harlan, 1824; *Dipsosaurus* Hallowell, 1854; *Iguana* Laurenti, 1768; *Sauromalus* Duméril, 1856.

Distribution.—Tropical and subtropical America from the southwestern United States and eastern Mexico south to southern Brazil and Paraguay; Galapagos Islands; Antilles; Fiji and Tonga Islands (Fig. 21).

Comment.—Iguanidae corresponds to the "iguanines" of Etheridge (1964) and Etheridge and de Queiroz (1988) and Iguaninae of de Queiroz (1987). For a formal infrafamilial taxonomy see de Queiroz (1987) (See discussion in "Results").

OPLURIDAE MOODY, 1983

1843. Doryphori Fitzinger, Syst. Rept., 1:17. Type genus: "*Doryphorus* (Cuv.)." See comment.

1983a. Opluridae Moody, Adv. Herpetol. Evol. Biol.:202. Type genus: *Oplurus* Cuvier, 1829.

Characterization.—(1) maxillae not meeting anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen not enlarged; (3) skull roof strongly rugose; (4) jugal and squamosal not broadly juxtaposed; (5) parietal roof trapezoidal; (6) parietal foramen in frontoparietal suture; (7) supratemporal sits on medial side of supratemporal process of parietal; (8) nuchal endolymphatic sacs not penetrating nuchal musculature; (9) dentary not expanded onto labial face of coronoid; (10) labial blade of coronoid poorly developed or absent; (11) anterior surangular foramen above posteriormost extent of dentary; (12) Meckel's groove variably fused or not; (13) splenial relatively short anteriorly; (14) dentary and maxillary teeth pleurodont, not fused to underlying bone in adults; (15) palatine teeth present in some *Oplurus*, otherwise absent; (16) pterygoid teeth present; (17) posterior process of interclavicle not invested by sternum far anteriorly; (18) caudal autotomy fracture planes present, with transverse processes anterior to fracture planes; (19) posterior coracoid fenestra absent; (20) sternal fontanelles very small or absent; (21) sternal ribs 3 or 4; (22) postxiphisternal inscriptional ribs appear in the form of paired splints, isolated from the dorsal ribs and not confluent medially; (23) interparietal scale not enlarged; (24) mid-dorsal scale row absent (*Oplurus*) or present, enlarged (*Chalarodon*); (25) gular fold complete medially; (26) femoral

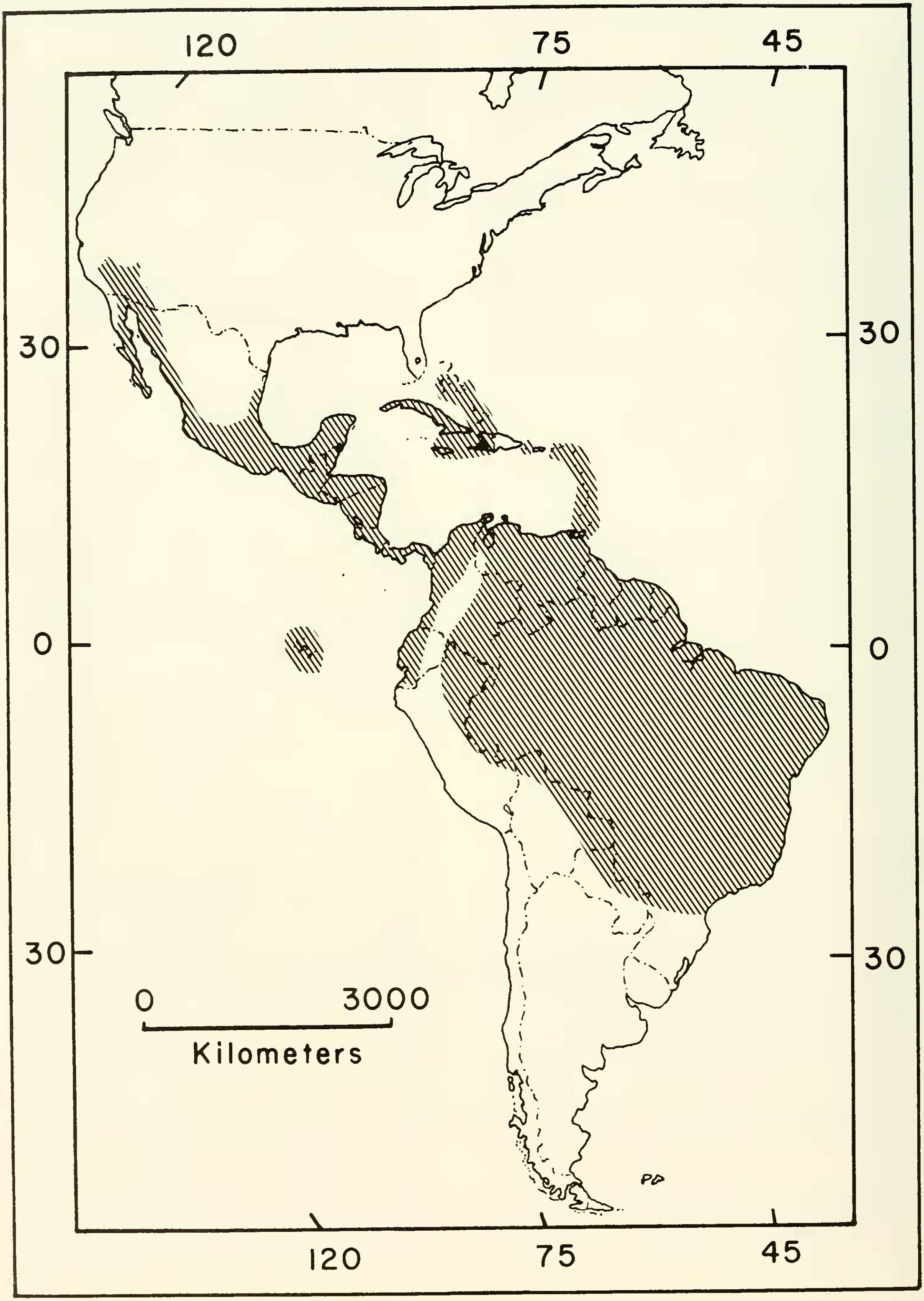

Fig. 21. Distribution of Iguanidae, excluding Fijian and Tongan regions.

pores absent; (27) spinulate scale organs present; (28) primitive nasal apparatus; nasal vestibule relatively short, straight; concha present, free; (29) hemipenes unicapitate, unisulcate; (30) colic septa absent.

Content.—*Chalarodon* Duméril and Bibron, 1837; *Oplurus* Cuvier, 1829.

Distribution.—Western and Central Madagascar; Comoro Islands.

Comment.—Opluridae corresponds to the "oplurines" of Smith *et al.* (1973), Etheridge *in* Paull *et al.* (1976), and Etheridge and de Queiroz (1988). The nomenclatural status of Doryphoridae is arguable. Fitzinger (1843) erected the family Doryphori based on "*Doryphorus* (Cuv.)," the parentheses around Cuvier meaning, in Fitzinger's words (1843:15) "Citata uncinis inclusa auctores indicant, qui genus quidem nominaverunt, sed non stricte in eodem sensu proposuerunt" (=the parentheses enclose the indicated authors of the genus name, although the names are not used strictly in the original sense as proposed). The problem lies in that *Doryphorus* Cuvier has a type species set by monotypy, *Stellio brevicaudatus* Latreille, 1802 (= *Uracentron azureum*), not included in Fitzinger's sense of the genus. Fitzinger regarded the type species of *Doryphorus* to be *Hoplurus maximiliani* Duméril and Bibron, 1837 (=*Oplurus cyclurus* Merrem, 1820). Article 65(b) of the International Code of Zoological Nomenclature (1985) requires that such "altered concept" problems be referred to the Commission for ruling. However, pending application, we employ the name Opluridae herein, rather than resurrecting a name beset with nomenclatural difficulties.

PHRYNOSOMATIDAE FITZINGER, 1843

1843. Phrynosomata Fitzinger, Syst. Rept., 1:17. Type genus: *Phrynosoma* Wiegmann, 1828.

1971. Sceloporinae Kästle, Grzimek's Tierleben, 6:181–182. Type genus: *Sceloporus* Wiegmann, 1828.

Characterization.—(1) maxillae not meeting anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen not enlarged; (3) skull roof not strongly rugose; (4) jugal and squamosal not broadly juxtaposed; (5) parietal roof trapezoidal; (6) parietal foramen in frontoparietal suture; (7) supratemporal sits on lateral side of supratemporal process of parietal; (8) nuchal endolymphatic sacs not penetrating nuchal musculature; (9) dentary not expanded onto labial face of coronoid; (10) labial blade of coronoid poorly developed or absent; (11) anterior surangular foramen above posteriormost extent of dentary; (12) Meckel's groove not fused; (13) splenial relatively long anteriorly; (14) dentary and maxillary teeth pleurodont, not fused to underlying bone in adults; (15) palatine teeth absent; (16) pterygoid teeth absent; (17) posterior process of interclavicle invested by sternum far anteriorly; (18) caudal autotomy fracture planes present (except in *Phrynosoma*), with transverse processes anterior to fracture planes; (19) posterior coracoid fenestra absent; (20) sternal fontanelle enlarged and median; (21) sternal ribs number 3 or 4 (*Petrosaurus*); (22) postxiphisternal inscriptional ribs short; (23) interparietal scale large (except in *Phrynosoma* and *Uma*); (24) mid-dorsal scale row absent; (25) gular fold complete medially (except *Sceloporus*); (26) femoral pores present; (27) spinulate scale organs absent; (28) sink-trap nasal apparatus; nasal vestibule long, straight, supported by elongated septomaxilla; concha absent (29) hemipenes unicapitate, unisulcate, with enlarged posterior lobe; (30) colic septa absent.

Content.—*Callisaurus* Blainville, 1835; *Holbrookia* Girard, 1851 (including *Cophosaurus* Troschel, 1852); *Petrosaurus* Boulenger, 1885; *Phrynosoma* Wiegmann, 1828; *Sceloporus* Wiegmann, 1828 (including *Sator* Dickerson, 1919); *Uma* Baird, 1858; *Urosaurus* Hallowell, 1854; *Uta* Baird and Girard, 1852.

Distribution.—Southern Canada through the USA to Panama (Fig. 22).

Comment.—Phrynosomatidae corresponds to the "sceloporines" of Savage (1958), Etheridge (1964), Presch (1969), and Etheridge and de Queiroz (1988).

POLYCHRIDAE FITZINGER, 1843

1826. Pneustoidea Fitzinger, Neue Classif. Rept.:11. Type genus: Not stated. See comment.

1843. Polychri Fitzinger, Syst. Rept., 1:16. Type genus: *Polychrus* Cuvier, 1817.

1843. Dactyloae Fitzinger, Syst. Rept., 1:17.

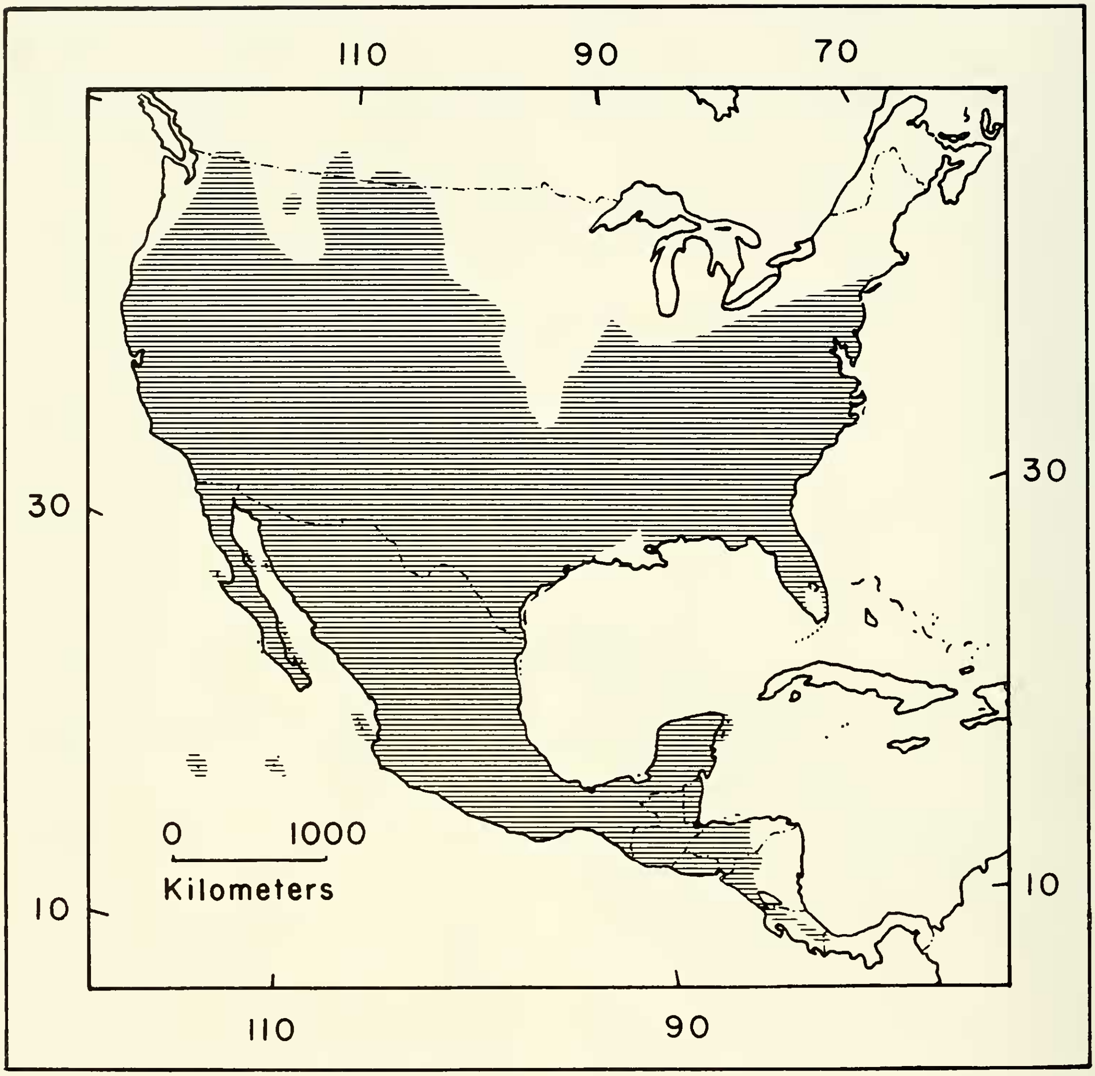

Fig. 22. Distribution of Phrynosomatidae.

Type genus: *Dactyloa* Wagler, 1830 (=*Anolis* Daudin, 1802).

1843. Draconturae Fitzinger, Syst. Rept., 1:17. Type genus: "*Dracontura* Wagler" (=*Draconura* Wagler, 1830 =*Anolis* Daudin, 1802).

1864. Anolidae Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:227. Type genus: *Anolis* Daudin, 1802.

Characterization.—(1) maxillae not meeting anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen not enlarged; (3) skull roof strongly rugose (except in *Diplolaemus* and some *Anolis*); (4) jugal and squamosal not broadly juxtaposed; (5) parietal roof trapezoidal or V or Y-shaped; (6) parietal foramen normally in frontoparietal suture (in parietal in some *Anolis* and lacking in some *Polychrus*); (7) supratemporal sits on lateral side of supratemporal process of parietal; (8) nuchal endolymphatic sacs penetrating nuchal musculature; (9) dentary not expanded onto labial face of coronoid; (10) labial blade of coronoid variable, from well-developed to absent; (11) anterior surangular foramen above posteriormost extent of dentary; (12) Meckel's groove fused; (13) splenial relatively to very short anterior to level or apex of coronoid; (14) dentary and maxillary teeth pleurodont, not fused to underlying bone in adults; (15) palatine teeth present (except *Polychrus* and anoles other than *Chamaeolis*); (16) pterygoid teeth present (except some *Polychrus*); (17) posterior process of interclavicle variably invested by sternum far anteriorly; (18) caudal autotomy fracture planes present or absent, with transverse processes anterior or posterior to fracture planes, if present; (19) posterior coracoid fenestra small or absent; (20) sternal fontanelles very small or absent; (21) sternal ribs number 2, 3, or 4; (22) postxiphisternal inscriptional ribs long, confluent medially; (23) interparietal scale not enlarged; (24) mid-dorsal scale row variable; (25) gular fold complete medially (except *Polychrus* and anoles); (26) femoral pores absent (except *Polychrus*); (27) spinulate scale organs present (except *Polychrus*); (28) primitive nasal apparatus; nasal vestibule relatively short, straight; concha present or absent; (29) hemipenes variable—plesiomorphically bicapitate, bisulcate (unicapitate in some *Anolis*); (30) colic septa absent.

Content.—*Anisolepis* Boulenger, 1885 (including *Aptycholaemus* Boulenger, 1891, *fide* Etheridge and Williams, unpubl.); *Anolis* Daudin, 1802; *Chamaeolis* Cocteau, 1838; *Chamaelinorops* Schmidt, 1919; *Diplolaemus* Bell, 1843; *Enyalius* Wagler, 1830; *Leiosaurus* Duméril and Bibron, 1837 (including *Aperopristis* Peracca, 1897); *Phenacosaurus* Barbour, 1920; *Polychrus* Cuvier, 1817; "*Pristidactylus*" Fitzinger, 1843; *Urostrophus** Duméril and Bibron, 1837.

Distribution.—Southern North America to southern South America; West Indies (Fig. 23).

Comment.—Polychridae corresponds in content to the "anoloids" of Etheridge and Williams (1985) and Etheridge and de Queiroz (1988).

We select Polychri Fitzinger, 1843, to have priority over Dactyloae Fitzinger, 1843, and Draconturae Fitzinger, 1843, under the provisions of Article 24 ("Principle of the First Revisor") and Recommendation 24A of the International Code of Zoological Nomenclature (1985).

Apparently owing to a typographic error, Fitzinger (1826) did not mention the apparent type genus of Pneustidae, *Pneustes* Merrem, 1820 (type species: *P. prehensilis* Merrem, 1820). *Pneustes prehensilis* is a *nomen dubium* (Smith, 1957), considered to be a synonym of *Laemanctus vautieri* (=*Urostrophus vautieri*) by Fitzinger (1843:62), but probably a synonym of *Polychrus acutirostris* Spix, 1825 (P. E. Vanzolini, *in litt.*). Note, however, that certain features noted in the diagnosis of *Pneustes prehensilis* (e.g., four toes on each foot) render it a *nomen dubium*. Not having an "express reference" or "inference in context" to a type genus in Fitzinger's work prevents Pneustoidea from being an available family group name (Art. 11.f.i.1; International Code of Zoological Nomenclature, 1985), as does the status of *Pneustes* as a *nomen dubium*.

We do not follow Guyer and Savage (1986) in recognizing the nominal genera *Ctenonotus* Fitzinger, 1843, *Dactyloa* Wagler, 1830, *Norops* Wagler, 1830, and *Semiurus* Fitzinger, 1843, as distinct from *Anolis* because the phylogenetic basis for recognition of these other taxa is arguable (Cannatella and de Queiroz, 1989).

TROPIDURIDAE BELL, 1843

1843. Tropiduridae Bell, Zool Voy. Beagle:1. Type genus: *Tropidurus* Wied-Neuwied, 1825. See comment under Tropidurinae.

1843. Ptychosauri Fitzinger, Syst. Rept., 1:16. Type genus: *Ptychosaurus* Fitzinger, 1843 (=*Plica* Gray, 1831).

1843. Steirolepides Fitzinger, Syst. Rept., 1:17. Type genus: *Steirolepis* Fitzinger, 1843 (=*Tropidurus* Wied-Neuwied, 1825).

1843. Heterotropides Fitzinger, Syst. Rept., 1:17. Type genus: *Heterotropis* Fitzinger, 1843 (a *nomen dubium*) (=?*Stenocercus* Duméril and Bibron, 1837).

Characterization.—(1) maxillae not meeting anteromedially behind palatal portion of premaxilla; (2) lacrimal foramen not enlarged;

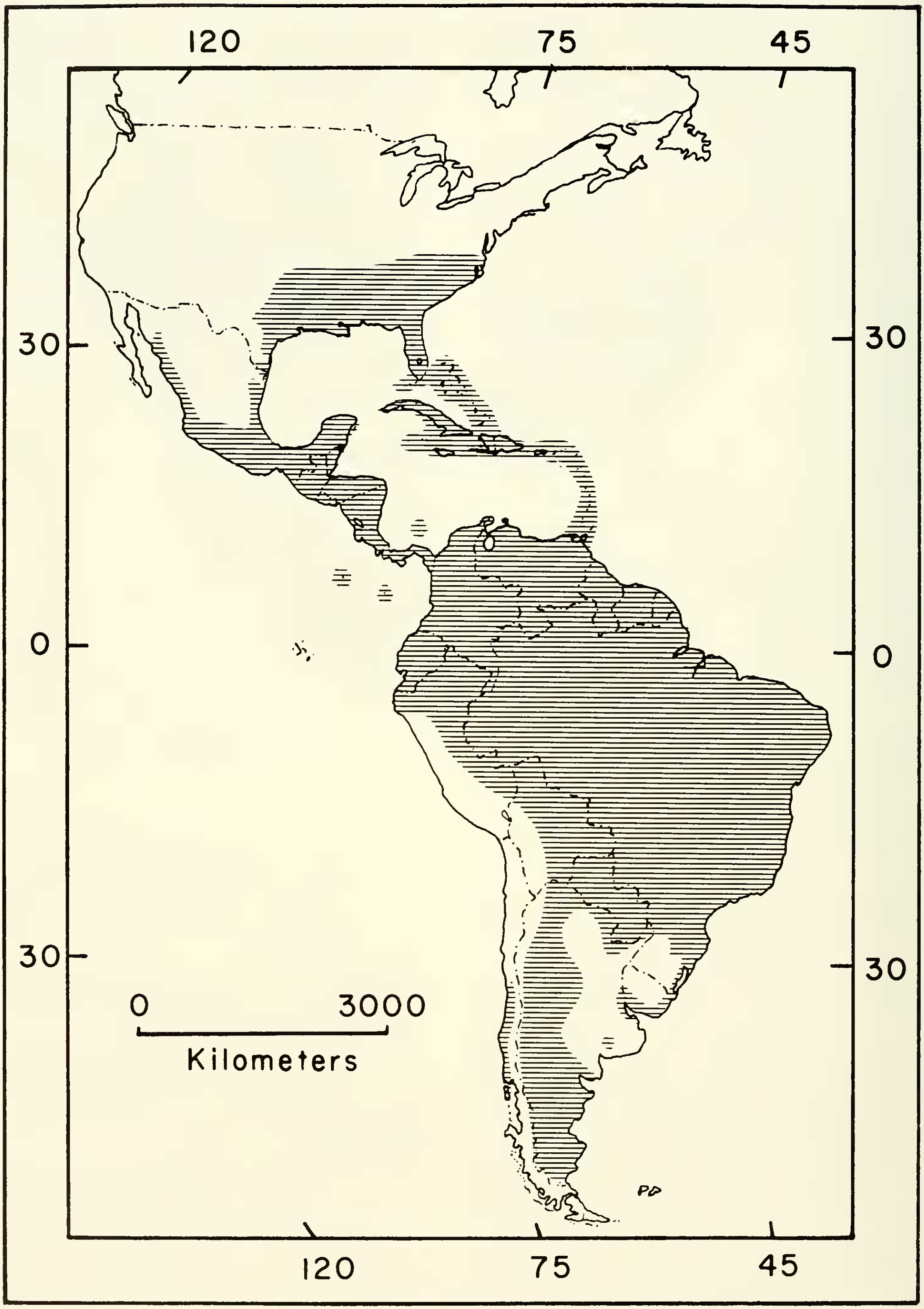

Fig. 23. Distribution of Polychridae.

(3) skull roof not strongly rugose; (4) jugal and squamosal not broadly juxtaposed; (5) parietal roof trapezoidal (or V-shaped in *Leiocephalus*); (6) parietal foramen in frontoparietal suture or absent; (7) supratemporal sits on lateral or medial side, or in ventral groove of supratemporal process of parietal; (8) nuchal endolymphatic sacs not penetrating nuchal musculature; (9) dentary not expanded onto labial face of coronoid; (10) labial blade of coronoid poorly developed or absent (Tropidurinae) or well-developed (Liolaeminae, Leiocephalinae); (11) anterior surangular foramen superior to posteriormost extent of dentary; (12) Meckel's groove variably fused (except some *Phymaturus, Ctenoblepharys,* and some *Liolaemus*); (13) splenial very short anteriorly (except in some liolaemines); (14) dentary and maxillary teeth pleurodont, not fused to underlying bone in adults; (15) palatine teeth absent; (16) pterygoid teeth present (except some *Leiocephalus,* some "*Stenocercus*"); (17) posterior process of interclavicle not invested by sternum far anteriorly (except in the "*Tropidurus*" group); (18) caudal autotomy fracture planes present, with transverse processes anterior to fracture planes; (19) posterior coracoid fenestra present (except in *Phymaturus* and *Ctenoblepharys*); (20) sternal fontanelles median and enlarged (except in some "*Tropidurus*"); (21) sternal ribs number 3 or 4; (22) postxiphisternal inscriptional ribs short (long in some "*Ophryoessoides*" and some "*Stenocercus*"); (23) interparietal scale variable, enlarged only in the "*Tropidurus*" group of Tropidurinae; (24) mid-dorsal scale row generally present (except in Liolaeminae, some "*Stenocercus,*" and some members of the "*Tropidurus*" group); (25) gular fold incomplete medially; (26) femoral pores absent; (27) spinulate scale organs absent; (28) generally primitive nasal apparatus; nasal vestibule relatively short, straight; concha present, generally free, but fused to the roof of the nasal chamber in Tropidurinae; (29) hemipenes variable; (30) colic septa absent.

Content.—Leiocephalinae new subfamily; Liolaeminae new subfamily; and Tropidurinae Bell, 1843.

Distribution.—The Bahama Islands, Cuba and Hispaniola and associated banks; Cayman Islands; South America, excluding northern Colombia and northern Venezuela, southward to northern Tierra del Fuego; Galapagos Islands (Fig. 24).

Comment.—Tropiduridae corresponds to the "tropidurines" of Etheridge (1966) and Etheridge and de Queiroz (1988).

LEIOCEPHALINAE NEW SUBFAMILY

Type genus.—*Leiocephalus* Gray, 1825.

Characterization.—(1) premaxillary spine overlapped by nasals; (2) parietal table Y or V-shaped (shared with some iguanids and anoles); (3) large labial blade of coronoid; (4) anterior extent of splenial extending more than ⅙ length of precoronoid length of mandible; (5) well-developed anterior process of interclavicle; (6) interparietal scale not enlarged; (7) no preanal pores; (8) primitive nasal condition, nasal vestibule short and straight, nasal concha not fused to roof of nasal chamber; (9) unicapitate, unisulcate hemipenes.

Content.—*Leiocephalus* Gray, 1825.

Distribution.—Bahama Islands, Cuba and Hispaniola and associated banks (extinct on Jamaica, Puerto Rico, Barbuda, Antigua, Anguilla, Martinique, and Guadeloupe [Pregill *et al.*, 1988]); Cayman Islands (Fig. 24).

LIOLAEMINAE NEW SUBFAMILY

Type genus.—*Liolaemus* Wiegmann, 1834.

Characterization.—(1) premaxillary spine overlapped by nasals (except in some *Phymaturus*); (2) parietal table not Y or V-shaped; (3) large labial blade of coronoid; (4) anterior extent of splenial extending more than ⅙ length of precoronoid length of mandible; (5) poorly developed anterior process of interclavicle; (6) interparietal scale not enlarged; (7) preanal pores (except in some species of *Liolaemus*); (8) S-nasal condition, nasal concha not fused to roof of nasal chamber; (9) weakly bicapitate, unisulcate hemipenes.

Content.—*Ctenoblepharys* Tschudi, 1845; *Liolaemus* Wiegmann, 1834; *Phymaturus* Gravenhorst, 1838 (see comment).

Distribution.—Coastal and Andean Peru southward through Bolivia, Chile, and Argentina to northern Tierra del Fuego and the coasts of Uruguay and southeastern Brazil (Fig. 24).

Comment.—We have not followed Cei and

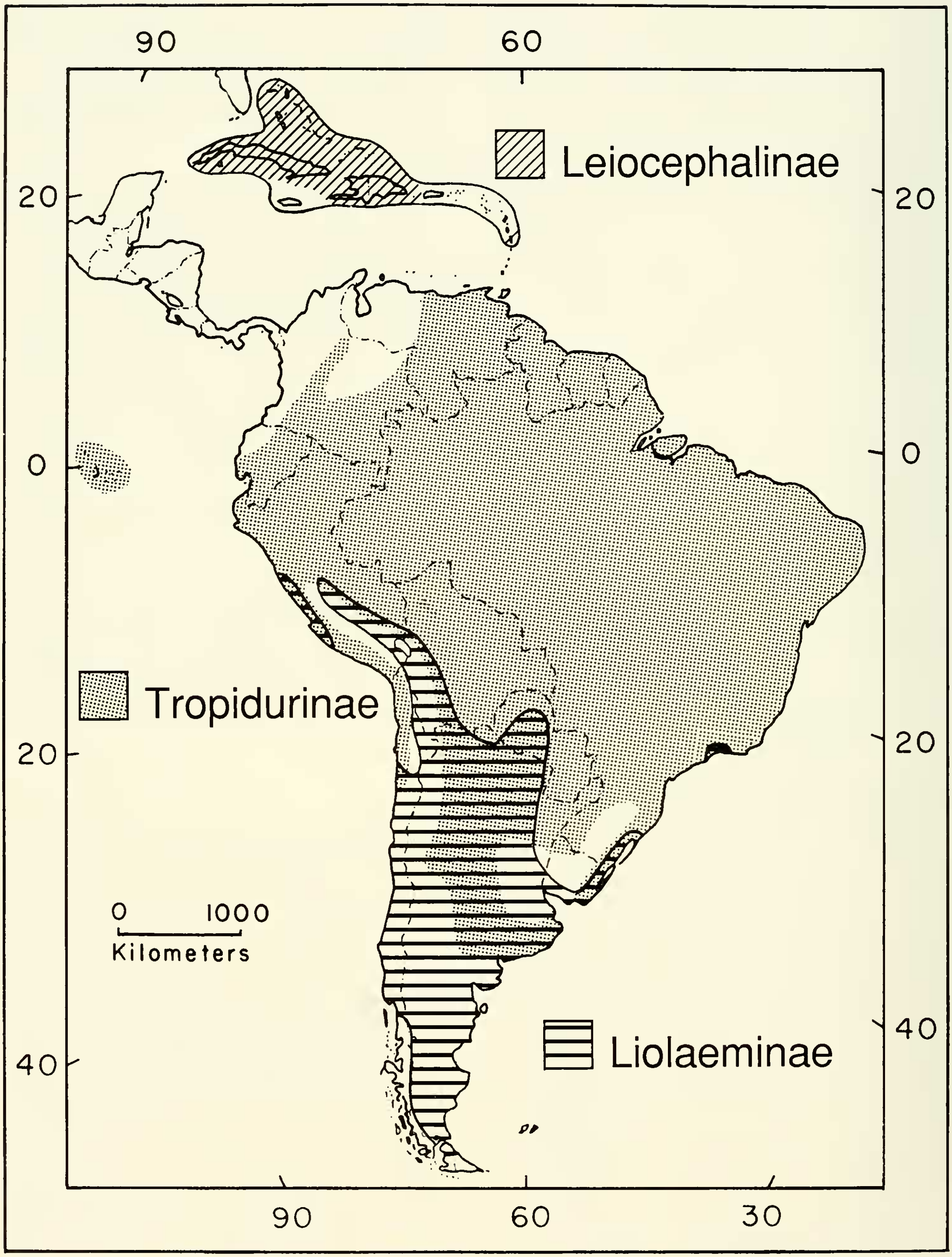

Fig. 24. Distribution of Tropiduridae, including subfamilies. The solid line surrounding the distribution of Leiocephalinae indicates that late Pleistocene–Early Holocene distribution of that taxon.

Lescure (1985) and Cei (1986) in the use of *Centrura* Bell, 1843, instead of *Phymaturus* Molina, 1768. As noted by Cei and Lescure (1985), the nomenclatural confusion was due to misidentification of type species in the original description of *Phymaturus*. In these cases it is required that traditional usage be maintained and that the International Commission of Zoological Nomenclature be petitioned to resolve the problem (Art. 70b; International Code of Zoological Nomenclature, 1985).

TROPIDURINAE BELL, 1843

1843. Tropiduridae Bell, Zool Voy. Beagle:1. Type genus: *Tropidurus* Wied-Neuwied, 1825. See comment.
1843. Ptychosauri Fitzinger, Syst. Rept., 1:16. Type genus: *Ptychosaurus* Fitzinger, 1843 (=*Plica* Gray, 1831).
1843. Steirolepides Fitzinger, Syst. Rept., 1:17. Type genus: *Steirolepis* Fitzinger, 1843 (=*Tropidurus* Wied-Neuwied, 1825).
1843. Heterotropides Fitzinger, Syst. Rept., 1:17. Type genus: *Heterotropis* Fitzinger, 1843 (a *nomen dubium*) (=?*Stenocercus* Duméril and Bibron, 1837).

Characterization.—(1) premaxillary spine not overlapped by nasals; (2) parietal table not Y or V-shaped; (3) no labial blade of coronoid; (4) splenial extending anteriorly no more than ⅙ length of precoronoid length of mandible; (5) anterior process of interclavicle poorly developed or absent; (6) interparietal scale enlarged; (7) no preanal pores; (8) nasal concha fused to roof of nasal chamber, nasal vestibule relative short and straight; (9) bisulcate, weakly to strongly bicapitate hemipenes.

Content.—"*Ophryoessoides*" Duméril, 1851; *Plica*[8] Gray, 1831; *Proctotretus* Duméril and Bibron, 1837; "*Stenocercus*" Duméril and Bibron, 1837; *Strobilurus* Wiegmann, 1834; *Tapinurus* Amaral, 1933; "*Tropidurus*" Wied-Neuwied, 1825; *Uracentron* Kaup, 1826; *Uranoscodon* Kaup, 1825.

Distribution.—South America, excluding northern Colombia and northern Venezuela, southward to northern Chile and central Argentina; Galapagos Islands (Fig. 24).

Comment.—We follow Smith and Grant (1958) in regarding Bell's (1843) publication of Tropiduridae to have priority over Fitzinger's (1843) publication of Steirolepides, Ptychosauri, and Heterotropides.

SUMMARY

A phylogenetic analysis of Iguania was performed using 67 transformation series containing 147 characters of osteology, dentition, squamation, internal nasal structure, musculature, and hemipenes. For analysis, 35 taxonomic units, representing all iguanians, were used. Data analysis was performed using PAUP version 2.4.1 (Swofford, 1985) and Hennig86 version 1.5 (Farris, 1988). No evidence of monophyly was discovered for "Iguanidae" and only ambiguous evidence for the monophyly of Agamidae*, although some lines of evidence support the view that these nominal taxa are paraphyletic. The historical reality (=monophyly) of Chamaeleonidae was highly corroborated. A total of 225 alternative supported tree topologies were discovered (208 steps, C.I.=0.385). These alternative topologies were produced by 12 unrooted networks, that could be variously rooted to produce 18 trees of nine major monophyletic groups (acrodonts [=Agamidae* + Chamaeleonidae], anoloids, basiliscines, crotaphytines, iguanines, morunasaurs, oplurines, sceloporines, and tropidurines), and alternative topologies within these monophyletic groups. These alternatives are variably dependent on unrooted network topology. Two topologies were discovered within

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[8] With the removal of the *nomen oblitum* rule (Art. 23b of the 1961 International Code) in the 1985 International Code, the oldest name available for this taxon becomes *Hypsibatus* Wagler, 1830. However, ongoing work by Frost will obviate this anomaly. Therefore, we retain *Plica* for purposes of this publication.

the *Liolaemus* group of the tropidurines, three in the sceloporines, two in the acrodonts, and three in the anoloids. In order to obviate the possibility of paraphyly and to reform named but misleading groupings into historically real components, and to demonstrate our ignorance of intergroup relationships, "Iguanidae" was partitioned into 8 taxa *sedis mutabilis*, ranked as families: Corytophanidae Fitzinger, 1843 (former basiliscines); Crotaphytidae Smith and Brodie, 1982 (former crotaphytines); Hoplocercidae new name (former morunasaurs); Iguanidae Oppel, 1811 (former iguanines); Opluridae Moody, 1983; Phrynosomatidae Fitzinger, 1843 (former sceloporines); Polychridae Fitzinger, 1843 (former anoloids); Tropiduridae Bell, 1843 (former tropidurines). Within Tropiduridae three subfamilies were recognized *sedis mutabilis*: Leiocephalinae new name; Liolaeminae new name; Tropidurinae Bell, 1843. Agamidae* may be paraphyletic with respect to Chamaeleonidae; to correct this, three monophyletic subfamilies (Chamaeleoninae Rafinesque, 1815; Agaminae Spix, 1825; and Leiolepidinae Fitzinger, 1843) were recognized, *sedis mutabilis*, within a reconstituted Chamaeleonidae Rafinesque, 1815 (equivalent to Acrodonta Cope, 1864), that is a highly corroborated monophyletic group. Relationships among the family-groups are poorly resolved, and much of the topological differences between discovered trees was because of this lack of resolution.

LITERATURE CITED

Arnold, E. N. 1981. Estimating phylogenies at low taxonomic levels. Z. Zool. Syst. Evolutionsforsch., 19:1–35.

Arnold, E. N. 1984. Variation in the cloacal and hemipenial muscles of lizards and its bearing on their relationships. pp. 57–85 *In:* M. J. Ferguson (*ed.*), The structure, development and evolution of reptiles. Symp. Zool. Soc. London, 52.

Axtell, R. W. 1958. A monographic revision of the iguanid genus *Holbrookia*. Ph.D. Dissertation, Univ. Texas, Austin. 222 pp.

Axtell, R. W., and A. O. Wasserman. 1953. Interesting herpetological records from southern Texas and northern Mexico. Herpetologica, 9:1–6.

Bell, T. 1825. Description of a new species of lizard. Zool. J., London, 1825:457–460.

Bell, T. 1843. Zoology of the voyage of the H. M. S. Beagle, under the command of Captain Fitzroy, R. N., during the years 1832 to 1836. Edited and superintended by Charles Darwin . . . naturalist to the expedition. Part 5. Reptiles. vi + 51 pp., atlas. Smith, Elder & Co., London.

Böhme, W. 1988. Genitalmorphologie der Sauria: Funktionelle und stammesgeschichtliche Aspekte. Bonn. Zool. Monogr., 27:1–176.

Borsuk-Białynicka, M., and S. M. Moody. 1984. Priscagaminae, a new subfamily of the Agamidae (Sauria) from the Late Cretaceous of the Gobi Desert. Acta Palaeontol. Polon., 29:51–81.

Brooks, D. R., and E. O. Wiley. 1985. Theories and methods in different approaches to phylogenetic systematics. Cladistics, 1:1–12.

Camp, C. 1923. Classification of the lizards. Bull. Am. Mus. Nat. Hist., 48:289–481.

Cannatella, D. C., and K. de Queiroz. 1989. Phylogenetic systematics of the anoles: Is a new taxonomy warranted? Syst. Zool., 38:57–69.

Cei, J. M. 1979a. Remarks on the South American lizard *Liolaemus anomalus* Koslowsky, and the synonymy of *Phrynosaura werneri* Müller (Reptilia, Lacertilia, Iguanidae). J. Herpetol., 13:183–186.

Cei, J. M. 1979b. A reassessment of the genus *Ctenoblepharis* (Reptilia, Sauria, Iguanidae) with a description of a new subspecies of *Liolaemus multimaculatus* from western Argentina. J. Herpetol., 13:297–302.

Cei, J. M. 1986. Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. Mus. Reg. Sci. Nat. Torino, Monogr., 4:1–526.

Cei, J. M., and J. Lescure. 1985. Identité de *Lacerta palluma* Molina, 1782, et révalidation de *Centrura flagellifer* Bell, 1843 (Reptilia, Sauria). Bull. Mus. Natl. Hist. Nat., Paris, (4)7(A)2:175–183.

Cei, J. M., and J. A. Scolaro. 1982. A new species of the Patagonian genus *Vilcunia*, with remarks on its morphology, ecology, and distribution. J. Herpetol., 16:354–363.

Cooper, J. S., D. F. G. Poole, and R. Lawson. 1970. The dentition of agamid lizards with special reference to tooth replacement. J. Zool., London, 162:85–98.

Cope, E. D. 1864. On the characters of the higher groups of Reptilia Squamata—and especially of the Diploglossa. Proc. Acad. Nat. Sci. Philadelphia, 16:224–231.

Cope, E. D. 1900. The crocodilians, lizards and snakes of North America. Annu. Rep. U.S. Natl. Mus. for 1898:153–1270.

Cuvier, G. 1817. Le règne animal distribué d'après son organisation, pour servir de base d'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Vol. 2, Les reptiles, les poissons, les mollusques, et les aniélides. Deterville, Paris.

de Queiroz, K. 1982. The scleral ossicles of the sceloporine iguanids: A reexamination with comments on their phylogenetic significance. Herpetologica, 38:302–311.

de Queiroz, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Syst. Zool., 34:280–299.

de Queiroz, K. 1987. Phylogenetic systematics of iguanine lizards: A comparative osteological study. Univ. California Publ., Zool., 118:xii + 203.

de Queiroz, K., and M. T. Donoghue. 1988. Phylogenetic systematics and the species problem. Cladistics, 4:317–338.

Dixon, J. R., and J. W. Wright. 1975. A review of the lizards of the iguanid genus *Tropidurus* in Peru. Contrib. Sci. Nat. Hist. Mus. Los Angeles Cty., 271:1–39.

Donoghue, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. Bryologist, 88:172–181.

Donoso-Barros, R. 1972. Contribución al conocimiento del género *Ctenoblepharis* Tschudi y *Phrynosaura* Werner (Sauria: Iguanidae). Bol. Soc. Concepción, 44:129–144.

Donoso-Barros, R. 1973. Un nuevo saurio de Bolivia. Neotropica, Buenos Aires, 19(60):132–134.

Eldredge, N., and J. Cracraft. 1980. Phylogenetic patterns and the evolutionary process: Method and theory in comparative biology. Columbia Univ. Press, New York. 349 pp.

El Taubi, M. R., and H. M. Bishai. 1959. On the anatomy and histology of the digestive tract of the lizard *Uromastyx aegyptia* (Forskål). Bull. Fac. Sci. Cairo Univ., 34:13–50.

Estes, R. 1983a. Handbuch der Paläoherpetologie. Encyclopedia of paleoherpetology. Part 10A, Sauria terrestria, Amphisbaenia. Gustav Fischer, Stuttgart and New York. xxii + 249 pp.

Estes, R. 1983b. The fossil record and early distribution of lizards. pp. 365–398 *In:* A. G. J. Rhodin and K. Miyata (*eds.*), Advances in herpetology and evolutionary biology: Essays in the honor of Ernest E. Williams. Cambridge, Massachusetts.

Estes, R., J. Gauthier, and K. de Queiroz. 1988. Phylogenetic relationships within Squamata. pp. 119–282 *In:* R. Estes and G. Pregill (*eds.*), Phylogenetic relationships of lizard families: Essays commemorating Charles L. Camp. Stanford Univ. Press.

Estes, R., and L. I. Price. 1973. Iguanid lizard from the Upper Cretaceous of Brazil. Science, 180:748–751.

Etheridge, R. 1959. The relationships of the anoles (Reptilia: Sauria: Iguanidae): An interpretation based on skeletal morphology. Ph.D. Dissertation, Univ. Michigan, Ann Arbor. xiii + 236 pp.

Etheridge, R. 1964. The skeletal morphology and systematic relationships of sceloporine lizards. Copeia, 1964:610–631.

Etheridge, R. 1965. The abdominal skeleton of lizards in the family Iguanidae. Herpetologica, 21:161–168.

Etheridge, R. 1966. The systematic relationships of West Indian and South American lizards referred to the iguanid genus *Leiocephalus*. Copeia, 1966:79–91.

Etheridge, R. 1967. Lizard caudal vertebrae. Copeia, 1967:699–721.

Etheridge, R. 1969a. *Tropidogaster blainvillii* Duméril & Bibron, 1837 (Reptilia, Sauria): Proposed suppression under the Plenary Powers. Bull. Zool. Nomencl., 25:224–226.

Etheridge, R. 1969b. A review of the iguanid lizard genus *Enyalius*. Bull. Br. Mus. (Nat. Hist.), Zool., 18:231–260.

Etheridge, R., and K. de Queiroz. 1988. A phylogeny of Iguanidae. pp. 283–368 *In:* R. Estes and G. Pregill (*eds.*), Phylogenetic relationships of lizard families: Essays commemorating Charles L. Camp. Stanford Univ. Press.

Etheridge, R., and E. E. Williams. 1985. Notes on *Pristidactylus* (Squamata: Iguanidae). Breviora, 483:1–18.

Evans, S. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool. J. Linn. Soc., 70:203–264.

Evans, S. 1981. The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. Zool. J. Linn. Soc., 73:81–116.

Farris, J. S. 1970. Methods for computing Wagner trees. Syst. Zool., 19:83–92.

Farris, J. S. 1982. Outgroups and parsimony. Syst. Zool., 31:328–334.

Farris, J. S. 1988. Hennig86, Version 1.5. Reference. Privately printed.

Felsenstein, J. 1978. The number of evolutionary trees. Syst. Zool., 27:27–33.

Fitzinger, L. I. 1826. Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des k. k. Zoologischen Museum zu Wien. J. G. Hübner, Wien. vii + 66 pp.

Fitzinger, L. I. 1843. Systema Reptilium. Fasciculus primus. Amblyglossae. Baumüller and Seidel, Wien. 106 pp.

Frost, D. R. 1987. A phylogenetic analysis of the *Tropidurus* group of iguanian lizards, with comments on the relationships within the Iguania (Squamata). Ph.D. Dissertation, Univ. Kansas, Lawrence. xi + 350 pp.

Frost, D. R., and D. M. Hillis. 1990. Species in concept and practice: Herpetological applications. Herpetologica, 46: *in press.*

Gabe, M., and H. Saint Girons. 1969. Données histologiques sur les glandes salivaires des lépidosauriens. Mem. Mus. Natl. Hist. Nat., Paris, 58:1-112.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. pp. 1–55 *In:* K. Padian (*ed.*), The origin of birds and the evolution of flight. Mem. California Acad. Sci., 8:i–vii, 1–98.

Gauthier, J. A., R. Estes, and K. de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha. pp. 15–98 *In:* R. Estes and G. Pregill (*eds.*), Phylogenetic relationships of lizard families: Essays commemorating Charles L. Camp. Stanford Univ. Press.

Gorman, G. C., R. B. Huey, and E. E. Williams. 1969. Cytotaxonomic studies on some unusual iguanid lizards assigned to the genera *Chamaeleolis*, *Polychrus*, *Polychroides*, and *Phenacosaurus*, with behavioral notes. Breviora, 316:1–17.

Gray, J. E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. Ann. Philos., (2)10:193–217.

Gray, J. E. 1827. A description of new species of saurian reptiles; with a revision of the species of chamaeleons. Philos. Mag. Ann., (2)2:207–214.

Guyer, C., and J. M. Savage. 1986. Cladistic relationships among anoles. Syst. Zool., 35:509–531.

Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana. 263 pp.

Hillenius, D. 1986. The relationship of *Brookesia, Rhampholeon* and *Chamaeleo* (Chamaeleonidae, Reptilia). Bijdr. Dierkd., 56:29–38.

Hull, D. L. 1964. Consistency and monophyly. Syst. Zool., 13:1–11.

International Commission on Zoological Nomenclature. 1961. International Code of Zoological Nomenclature, adopted by the XV International Congress of Zoology. International Trust for Zoological Nomenclature, London. 176 pp.

International Commission on Zoological Nomenclature. 1985. International Code of Zoological Nomenclature, Third Edition, Adopted by the XX General Assembly of the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London. 338 pp.

Iverson, J. B. 1980. Colic modification in iguanine lizards. J. Morphol., 163:79–93.

Iverson, J. B. 1982. Adaptations for herbivory in iguanine lizards. pp. 60–76 *In:* G. M. Burghardt and A. S. Rand (*eds.*), Iguanas of the world. Noyes Publs., New York.

Jollie, M. T. 1960. The head skeleton of the lizard. Acta Zool., Stockholm, 41:1–64.

Jullien, R., and S. Renous-Lécuru. 1972. Variations du trajet du nerf ulnaire (ulnaris) et de l'innervation des muscles dorsaux de la jambe chez les lacertiliens (reptiles: squamates): Valeur systématique et application phylogénétique. Bull. Mus. Natl. Hist. Nat., (Zool.), Paris, 23(29):207–246.

Kästle, W. 1971. Die Leguan. pp. 181–206 *In:* H. C. B. Grzimek, H. Hediger, K. Klemmer, O. Kuhn, and H. Wermuth (*eds.*), Grzimek's Tierleben. vol. 6. Kriechthiere. Kindler, Zürich.

Klaver, C. J. J., and W. Böhme. 1986. Phylogeny and classification of the Chamaeleonidae (Sauria) with special reference to hemipenis morphology. Bonn. Zool. Monogr., 22:1–64.

Kluge, A. 1983. Cladistic relationships among gekkonid lizards. Copeia, 1983:465–475.

Kluge, A. 1985. Ontogeny and phylogenetic systematics. Cladistics, 1:13–28.

Kluge, A. 1989. Metacladistics. Cladistics, 5: *in press.*

Kluge, A. G., and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool., 18:1–32.

Lang, M. A. 1989. Phylogenetic and biogeographic patterns of basiliscine iguanians (Reptilia: Squamata: "Iguanidae"). Bonn. Zool. Monogr., 28:1–172.

Lapage, E. O. 1926. The septomaxillary of the Anura and Reptilia. J. Morphol. Physiol., 46:399–431.

Larsen, K. R., and W. W. Tanner. 1975. Evolution of the sceloporine lizards (Iguanidae). Gt. Basin Nat., 35:1–20.

Laurent, R. F. 1983a. Sinonimia del género *Pelusaurus* Donoso-Barros con *Liolaemus* (Sauria: Iguanidae). Bol. Assoc. Herpetol. Argentina, Buenos Aires, 1(1):9–10.

Laurent, R. F. 1983b. Contribución al conocimiento del estructura taxonómica del género *Liolaemus*

Wiegmann (Iguanidae). Bol. Assoc. Herpetol. Argentina, Buenos Aires, 1(3):16–18.

Laurent, R. F. 1984. On some iguanid genera related to or previously confused with *Liolaemus* Wiegmann. J. Herpetol., 18:357–373.

Laurent, R. F. 1985. Segunda contribución al conocimiento de la estructura taxonómica del género *Liolaemus* Wiegmann (Iguanidae). Cuad. Herpetol., Assoc. Herpetol. Argentina, Buenos Aires, 1(6):1037.

Laurenti, J. N. 1768. Specimen medicum exhibens synopsin reptilium emendatum cum experimentis circa venena et antidota reptilium austriacorum. Trattnern, Wien. 214 pp.

Lécuru, S. 1968. Remarques sur le scapulo-coracoide des lacertiliens. Ann. Sci. Nat., Zool., 10:475–510.

Lönnberg, E. 1902. On some points of relation between the morphological structure of the intestine and the diet of reptiles. Bih. Svenska Vetensk. Akad. Handl., (4)28(8):3–53.

Luke, C. 1986. Convergent evolution of lizard toe fringes. Biol. J. Linn. Soc., 27:1–16.

Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool., 33:83–103.

Maddison, W. P., and D. R. Maddison. 1987. MacClade. Version 2.1. User's Manual. Privately printed.

Malan, M. E. 1946. Contributions to the comparative anatomy of the nasal capsule and the Organ of Jacobson of the Lacertilia. Ann. Univ. Stellenbosch, 24A:69–137.

Medica, P. P., F. B. Turner, and D. D. Smith. 1973. Hormonal induction of color change in female leopard lizards, *Crotaphytus wislizenii*. Copeia, 1973:658–661.

Mittleman, M. B. 1942. A summary of the iguanid lizard genus *Urosaurus*. Bull. Mus. Comp. Zool., 2:105–181.

Moody, S. M. 1980. Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia). Ph.D. Dissertation, Univ. Michigan, Ann Arbor. 373 pp.

Moody, S. M. 1983a. The *rectus abdominis* muscle complex of the Lacertilia: Terminology, homology, and assumed presence in primitive iguanian lizards. pp. 195–212 *In:* A. G. C. Rhodin and K. Miyata (*eds.*), Advances in herpetology and evolutionary biology: Essays in honor of Ernest E. Williams. Cambridge, Massachusetts.

Moody, S. M. 1983b. Endolymphatic sacs in lizards: Phylogenetic and functional considerations. Abstract of paper presented as Soc. Stud. Amph. Rept. and Herpetol. League annual meeting, Salt Lake City, Utah.

Nelson, G. 1979. Cladistic analysis and synthesis: principles and definitions, with an historical note on Adanson's *Familles des Plantes* (1763–1764). Syst. Zool., 28:1–21.

Nopsca, F. 1923. Die Familien der Reptilien. Fortschr. Geol. Palaeont., Berlin, 2:1–210.

Northcutt, R. G. 1978. Forebrain and midbrain organization in lizards and its phylogenetic significance. pp. 11–64 *In:* N. Greenberg and P. D. MacLean (*eds.*), Behavior and neurology of lizards: An interdisciplinary colloquium. U.S. Dept. Health, Educ. Welfare, Publ. No. (ADM) 77–491.

Novacek, M. J. 1986. The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. Bull. Am. Mus. Nat. Hist., 183:1–111.

Nuñez, H., and J. L. Yañez. 1983. *Abas* y *Velosaura,* nuevos géneros de lagartos Iguanidae y proposiciones sistemáticas respecto de los géneros aliados (Reptilia: Squamata). Bol. Mus. Nac. Hist. Nat. Chile, Santiago, 40:97–105.

Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. J. Lindauer, München. xii+87pp.

Parsons, T. S. 1970. The nose and Jacobson's Organ. pp. 99–191 *In:* C. Gans (*ed.*), Biology of the Reptilia. vol. 2. Academic Press, London and New York.

Patterson, C. 1982. Morphological characters and homology. pp. 21–74 *In:* K. A. Joysey and A. E. Friday (*eds.*), Problems of phylogenetic reconstruction. Academic Press, London.

Patterson, R. 1987. Reptiles of southern Africa. C. Struik, Ltd., Cape Town. 128 pp.

Paull, D., E. E. Williams, and W. P. Hall. 1976. Lizard karyotypes from the Galapagos Islands: Chromosomes in phylogeny and evolution. Breviora, 441:1–31.

Peterson, J. A. 1983. The evolution of the subdigital pad in *Anolis*. I. Comparisons among the anoline genera. pp. 245–283 *In:* A. G. C. Rhodin and K. Miyata (*eds.*), Advances in herpetology and evolutionary biology: Essays in honor of Ernest E. Williams. Cambridge, Massachusetts.

Peterson, J. A., and E. E. Williams. 1981. A case history of retrograde evolution: the *onca* lineage in anoline lizards. II. Subdigital fine structure. Bull. Mus. Comp. Zool., 149:215–268.

Pregill, G. K. 1984. An extinct species of *Leiocephalus* from Haiti (Sauria: Iguanidae). Proc. Biol. Soc. Washington, 97:827–833.

Pregill, G. K., D. W. Steadmann, S. L. Olson, and F. B. Grady. 1988. Late Holocene fossil vertebrates from Burma Quarry, Antigua, Lesser Antilles. Smithson. Contrib. Zool., 463:i–iii+1–27.

Presch, W. 1969. Evolutionary osteology and relationships of the horned lizard genus *Phrynosoma* (family Iguanidae). Copeia, 1969:250–275.

Presch. W. 1988. Cladistic relationships within the Scincomorpha. pp. 471–492 *In:* R. Estes and G. Pregill (*eds.*), Phylogenetic relationships of lizard families: Essays commemorating Charles L. Camp. Stanford Univ. Press.

Rafinesque, C. S. 1815. Analyse de la nature ou Tableau de l'univers et des corps organisés. J. Barravecchia, Palermo. 224 pp.

Reeve, W. L. 1952. Taxonomy and distribution of the horned lizard *Phrynosoma*. Univ. Kansas Sci. Bull., 34:817–960.

Renous, S. 1979. Application de principes cladistiques à la phylogénèse et la biogéographie des lacertiliens. Gegenbaurs Morphol. Jahrb., 125:376–432.

Rieppel, O. 1981. The skull and jaw adductor musculature in chamaeleons. Rev. Suisse Zool., 88:433–445.

Rieppel, O. 1987. The phylogenetic relationships within the Chamaeleonidae, with comments on some aspects of cladistic analysis. Zool. J. Linn. Soc., 89:41–62.

Savage, J. M. 1958. The iguanid lizard genera *Urosaurus* and *Uta,* with remarks on related groups. Zoologica, New York, 43:41–54.

Schwenk, K. 1988. Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. pp. 569–598 *In:* R. Estes and G. Pregill (*eds.*), Phylogenetic relationships of lizard families: Essays commemorating Charles L. Camp. Stanford Univ. Press.

Slaby, O. 1981. Morphogenesis of the nasal capsule, the nasal epithelial tube and the organ of Jacobson in a member of the family Agamidae. Folia Morphol., Prague, 29:305–317.

Slaby, O. 1984. Morphogenesis of the nasal apparatus in a member of the genus *Chamaeleon* L. (Morphogenesis of the nasal capsule, the epithelial nasal tube and the organ of Jacobson in Sauropsida—VIII). Folia Morphol., Prague, 32:225–246.

Smith, H. M. 1946. Handbook of lizards. Comstock Publ. Co., New York. xxi + 557 pp.

Smith, H. M. 1957. Proposed use of the Plenary Powers to validate the generic name "Phrynosoma" Wiegmann, 1828 (Class Reptilia, Order Squamata), a name placed on the "Official List of Generic Names in Zoology" by the ruling given in "Opinion" 92. Bull. Zool. Nomencl., 13:267–279.

Smith, H. M., and E. D. Brodie, Jr. 1982. A guide to field identification—Reptiles of North America. Golden Press, New York. 240 pp.

Smith, H. M., and C. Grant. 1958. The proper names for some Cuban snakes: an analysis of dates of publication of Ramon de la Sagra's Historia Natural de Cuba, and of Fitzinger's Systema Reptilium. Herpetologica, 14:215–222.

Smith, H. M., G. Sinelnick, J. D. Fawcett, and R. E. Jones. 1973. A survey of the chronology of ovulation in anoline genera. Trans. Kansas Acad. Sci., 75:107–120.

Smith, M. A. 1932. Some notes on the monitors. J. Bombay Nat. Hist. Soc., 35:615–619.

Spix, J. B. von. 1825. Animalia nova sive species nova lacertarum quas in itinere per Brasiliam annis MDCCCXVII–MDCCCXX jussu et auspicius Maximiliani Josephi I Bavariae Regis suscepto collegit et descripsit Dr. J. B. de Spix. T. O. Weigel, Lipsiae. 26 pp.

Stebbins, R. C. 1943. Adaptations in the nasal passages for sand burrowing in the saurian genus *Uma*. Am. Nat., 77:38–52.

Stebbins, R. C. 1948. Nasal structure in lizards with reference to olfaction and conditioning of the inspired air. Am. J. Anat., 83:183–222.

Stevens, P. F. 1980. Evolutionary polarity of character states. Annu. Rev. Ecol. Syst., 11:333–358.

Stimie, M. 1966. The cranial anatomy of the iguanid *Anolis carolinensis* (Cuvier). Ann. Univ. Stellenbosch, 41A:243–268.

Sukhanov, V. B. 1961. Some problems of the phylogeny and systematics of Lacertilia (seu Sauria). Zool. Zh., 40:73–83. [English translation by Scintran, 1976. S. M. Moody and G. R. Zug (*eds.*). Smithson. Herpetol. Inform. Serv., 38:1–15.]

Swofford, D. L. 1985. PAUP—Phylogenetic Analysis Using Parsimony. Version 2.4.1. User's Manual. Privately Published.

Theobald, W. 1868. Catalogue of the reptiles of British Birma, embracing the provinces of Pegu, Martaban, and Tenasserim; with descriptions of new or little-known species. J. Linn. Soc., London, 10:4–67.

Watrous, L. E., and Q. D. Wheeler. 1981. The outgroup comparison method of character analysis. Syst. Zool., 30:1–11.

Wells, R. W., and C. R. Wellington. 1983. A synopsis of the class Reptilia in Australia. Austr. J. Herpetol., 1(3–4):73–129.

WERMUTH, H. 1967. Liste der rezenten Amphibien und Reptilien: Agamidae. Tierreich, 86:i–xiv, 1–127.

WILEY, E. O. 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. Syst. Zool., 28:308–337.

WILEY, E. O. 1981a. Convex groups and consistent classifications. Syst. Bot., 6:346–358.

WILEY, E. O. 1981b. Phylogenetics: The theory and practice of phylogenetic systematics. John Wiley and Sons, New York. 439 pp.

APPENDIX 1

DATA MATRIX OF IGUANIAN TERMINAL TAXA

SPHENO=Rhynchocephalia; SCLER=Scleroglossa; ANCES=Ancestor of ingroup (Iguania); PRISC=†*Priscagama**; AGAMI=agamids, excluding other agamid terminal taxa; UROMA=*Uromastyx*; LEIOL=*Leiolepis*; PHYSI=*Physignathus*; CHAME =chameleons; POLYC=*Polychrus*; ENYAL=*Enyalius*; PRIST="*Pristidactylus*"; PARAA=*Urostrophus** and *Anisolepis*; ANOLE=anoles; ENYLD ="*Enyalioides*"; BASIL=*Basiliscus*; CORYT=*Corytophanes*; LAEMA=*Laemanctus*; PETRO=*Petrosaurus*; SCELO=*Sceloporus*; UROSA=*Urosaurus*; UTA=*Uta;* PHRYN=*Phrynosoma*; SANDL=Sand lizards;PHYMA=*Phymaturus*; CTENO=*Ctenoblepharys;* LIOLA=*Liolaemus*; LEIOC=*Leiocephalus*; STENO="*Stenocercus*"; TROPI="*Tropidurus*"; URANO=*Uranoscodon*; CROTA=*Crotaphytus*; GAMBE=*Gambelia*; OPLUR=*Oplurus*; CHALA =*Chalarodon*; DIPSO=*Dipsosaurus*; BRACH=*Brachylophus*; IGUAN=iguanines, excluding *Dipsosaurus* and *Brachylophus*. Unordered transformations are: 12, 34, 36, 37, 40.

Appendix 1 continued.

Taxon	Character																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
SPHEN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	?	?
SCLER	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	?	0
ANCES	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?
PRISC	0	1	1	0	0	0	1	0	1	0	0	?	0	?	0	0	0	1	1	0	0	0
AGAMI	0	1	1	0	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	0	1	0
UROMA	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0
LEIOL	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0
PHYSI	0	1	1	0	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	0	1	0
CHAME	0	1	?	0	?	1	1	?	1	0	?	?	0	?	0	1	1	1	1	0	1	0
POLYC	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0
ENYAL	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0
PRIST	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0
PARAA	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0
ANOLE	0	0	0	0	0	0	1	0	0	?	0	0	1	1	0	0	1	0	0	1	2	1
ENYLD	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
BASIL	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	1	0	?	0	0
CORYT	0	0	0	0	0	0	0	1	1	3	1	0	1	0	0	0	0	1	0	1	1	?
LAEMA	0	0	0	0	0	0	1	1	0	3	?	0	0	0	0	0	0	1	0	1	0	0
PETRO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
SCELO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
UROSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
UTA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
PHRYN	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0
SANDL	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
PHYMA	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	1
CTENO	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1
LIOLA	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	?	?	1
LEIOC	1	0	0	0	0	0	?	0	0	1	0	0	0	0	0	0	1	0	0	1	2	1
STENO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	2	1
TROPI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	1	2	1
URANO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	2	1
CROTA	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
GAMBE	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
OPLUR	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	?	?	1
CHALA	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	?	1	1
DIPSO	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0
BRACH	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
IGUAN	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0

Appendix 1 continued.

	Character																					
Taxon	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
SPHEN	?	0	0	?	0	0	0	0	1	0	0	?	1	1	0	1	0	0	0	0	0	1
SCLER	?	0	0	0	1	0	0	?	0	1	0	?	?	?	0	?	0	0	0	0	0	?
ANCES	?	0	0	0	?	0	0	?	?	?	0	?	?	?	0	?	0	0	0	0	0	?
PRISC	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
AGAMI	0	0	0	1	1	1	0	1	1	1	0	0	1	1	2	2	1	0	1	0	0	1
UROMA	0	0	0	1	1	1	0	1	0	1	0	0	1	0	2	2	0	0	?	0	0	1
LEIOL	0	0	0	1	1	1	0	1	0	0	0	0	1	1	2	2	0	0	1	0	0	1
PHYSI	0	0	0	1	1	1	0	0	1	0	0	0	1	1	2	2	1	0	1	0	0	1
CHAME	0	0	0	1	1	1	?	?	?	?	0	0	?	1	0	?	2	1	1	0	0	1
POLYC	0	1	0	0	1	?	1	1	1	0	1	?	?	1	0	2	2	1	1	0	0	1
ENYAL	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	?	0	1	?	0	0	1
PRIST	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	?	0	1	0	0	0	1
PARAA	0	0	0	0	0	0	0	0	0	0	0	?	1	2	0	1	1	1	1	0	0	1
ANOLE	1	2	0	0	0	0	1	?	?	0	1	3	1	1	0	2	?	1	?	0	0	1
ENYLD	0	0	1	0	1	0	0	0	0	0	0	0	?	1	0	1	0	1	0	0	0	1
BASIL	0	0	0	0	1	0	0	0	0	0	0	2	1	1	0	1	0	0	0	0	0	0
CORYT	0	0	0	0	1	0	0	0	1	0	0	2	1	1	0	1	0	0	1	0	0	1
LAEMA	0	0	0	0	1	0	0	0	0	0	0	2	1	1	0	1	0	0	1	0	0	1
PETRO	0	?	0	0	1	1	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0
SCELO	0	1	0	0	1	1	0	1	0	0	1	0	0	1	1	1	1	0	0	1	0	0
UROSA	0	1	0	0	1	1	0	1	0	0	1	0	1	1	1	1	1	0	0	1	0	0
UTA	0	1	0	0	1	1	0	1	0	0	1	0	1	1	1	1	1	0	0	1	0	0
PHRYN	0	1	0	0	1	1	0	1	0	0	1	0	0	1	1	1	1	0	0	0	0	0
SANDL	0	1	0	0	1	1	0	1	0	0	1	0	0	1	1	1	1	0	0	?	0	0
PHYMA	1	0	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	?
CTENO	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
LIOLA	1	0	0	0	1	0	0	?	0	0	0	0	1	0	1	?	?	0	0	0	0	0
LEIOC	1	1	0	0	1	?	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0
STENO	0	2	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
TROPI	1	2	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	0	0
URANO	1	2	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	0	1
CROTA	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
GAMBE	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
OPLUR	?	?	0	0	?	0	0	0	0	0	0	0	0	1	0	2	0	2	0	0	1	0
CHALA	0	2	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	2	0	0	1	0
DIPSO	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0
BRACH	0	0	1	0	1	0	1	0	0	0	0	1	0	1	0	2	0	1	1	0	0	1
IGUAN	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	2	0	?	0	0	0	1

Appendix 1 continued.

	CHARACTER																						
TAXON	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67
SPHEN	1	0	0	1	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	0	0	0
SCLER	?	1	0	0	0	0	0	0	0	0	0	0	0	?	0	?	?	0	0	0	0	0	0
ANCES	?	?	0	?	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	0	0	0
PRISC	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
AGAMI	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	?	0	1
UROMA	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1
LEIOL	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1
PHYSI	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	?
CHAME	1	0	1	1	0	0	?	?	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1
POLYC	1	?	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0	0	0	0	0
ENYAL	?	0	0	1	0	1	?	1	0	0	0	?	0	0	1	0	2	0	0	1	0	0	?
PRIST	0	0	0	1	0	1	?	1	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0
PARAA	?	1	0	1	0	0	1	1	0	0	0	?	0	0	1	0	2	0	0	0	0	0	?
ANOLE	1	?	1	1	0	0	1	1	0	0	0	1	0	0	1	0	2	0	0	0	0	0	1
ENYLD	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
BASIL	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
CORYT	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	?
LAEMA	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	?
PETRO	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
SCELO	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	1	0
UROSA	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	1	0
UTA	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
PHRYN	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
SANDL	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0
PHYMA	?	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
CTENO	1	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	?
LIOLA	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
LEIOC	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
STENO	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	?	0
TROPI	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	0
URANO	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	1	0	0	?
CROTA	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
GAMBE	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
OPLUR	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
CHALA	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	?
DIPSO	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	?
BRACH	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	?
IGUAN	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0

APPENDIX 2

Apomorphy lists for tree in Figure 9. See legend of Appendix 1 for abbreviations used. Asterisks note character shifts that are of ambiguous placement. Characters from unpolarized or unordered transformations are noted by a "U." Daggers note other characters (not an exhaustive list) not used in the analysis.

Stem	Transformation Series	Ancestral Character	Derived Character
PRISC	* 6	1	0
AGAMI	U 32	0	1
UROMA	5	0	1
	U 32	0	1
	U 36	1	0
	65	0	1
LEIOL	U 62	0	1
PHYSI	U* 30	1	0
	57	1	0
CHAME	39	1	2
	47	0	1
	* 48	0	1
	U 58	0	1
	†supratemporal reduced to small splint not in contact with parietal (Rieppel, 1981).		
	†pterygoid fails to meet quadrate (Rieppel, 1981).		
	†zygodactylous feet.		
POLYC	5	0	1
	U 27	0	1
	U 48	1	0
	* 51	1	0
	52	1	0
	†acrocentric chromosomes acquired (Gorman *et al.*, 1969).		
	†fourth toe reduced, equals third in length (Cope, 1900; Etheridge and de Queiroz, 1988).		
ENYAL	U 17	0	1
	U 64	0	1
	†throat scales conical (Etheridge and de Queiroz, 1988).		
PRIST	* 13	1	0
	†supradigital scales become transversely expanded, lamellar-like (Etheridge and de Queiroz, 1988).		
	†proximal subdigital scales of toes 1–3 become enlarged (Etheridge and de Queiroz, 1988).		
PARAA	†sexual dichromatism lost (Etheridge and de Queiroz, 1988).		
ANOLE	U 17	0	1
	U 18	1	0
	U 21	1	2
	U 22	0	1
	U 23	0	1
	24	1	2
	67	0	1
	†distal pad raised under phalanges 2 and 3 (Etheridge and de Queiroz, 1988).		
ENYLD	U 18	1	0
	25	0	1
	†nasal scale enlarged (Etheridge, 1969b).		
BASIL	U 44	1	0
	U 45	1	0
CORYT	13	0	1
	U* 21	0	1
	U 31	0	1
LAEMA	7	0	1
	* 9	1	0

Appendix 2 continued.

STEM	TRANSFORMATION SERIES	ANCESTRAL CHARACTER	DERIVED CHARACTER
PETRO	U 38	1	0
	39	1	0
	†neural spines shortened (Etheridge, 1964).		
SCELO	U 35	1	0
	47	0	1
UROSA	†secondary cusps of posterior marginal teeth reduced (Etheridge and de Queiroz, 1988).		
UTA	†dark axillary spot (Mittleman, 1942) (homologous with those in sand lizards?).		
PHRYN	8	0	1
	†skull and head scales strongly modified (Reeve, 1952; Presch, 1969).		
	†phalanges lost from digits 4 and 5 of manus (Etheridge and de Queiroz, 1988).		
SANDL	66	0	1
	†labial scales elongated, obliquely oriented; lower jaw countersunk (Smith, 1946; Axtell, 1958).		
PHYMA	U 21	1	0
	U 30	0	1
	U 38	1	0
	39	1	0
CTENO	U 45	0	1
LIOLA	U 17	0	1
	U 36	1	0
LEIOC	10	0	1
	U 32	0	1
	†long, free xiphisternal rods curve forward to underly xiphisternal ribs (Etheridge, 1966).		
	†postrostral scales lost (Etheridge, 1966).		
STENO	U 23	1	0
	†extensive transverse hemipenial musculature (Arnold, 1984).		
TROPI	†lingual coronoid process of dentary present (Frost, 1987).		
	†articular surface of humeral head elevated (Frost,1987).		
URANO	U 44	0	1
	U 45	0	1
	47	1	0
	U 59	0	1
	†grebe-like toe fringes develop (Luke, 1986).		
CROTA	7	0	1
	41	0	1
GAMBE	†clavicular fenestrae (Etheridge and de Queiroz, 1988).		
	†intermuscular dermal pit on posterior surface of thigh (weakly developed in many *Crotaphytus*).		
OPLUR	U 38	1	2
	39	1	0
CHALA	9	0	1
	U 30	0	1
	U 46	1	0
DIPSO	11	0	1
	U 44	1	0
	U 45	1	0
BRACH	U 40	0	1
	41	0	1
IGUAN	10	0	1
	U 36	1	0
1	15	0	1
	U 31	0	1

Appendix 2 continued.

STEM	TRANSFORMATION SERIES	ANCESTRAL CHARACTER	DERIVED CHARACTER
2	* 3	1	0
	4	0	1
	* 6	1	0
	* 39	1	0
	U 46	0	1
3	7	1	0
	U 37	0	2
	U 40	1	0
4	* 8	0	1
	U 16	0	1
	U 17	0	1
	U* 21	0	1
	28	0	1
	* 67	0	1
5	2	0	1
	* 3	0	1
	9	0	1
	26	0	1
	U* 30	0	1
	U* 38	1	2
	* 39	0	1
	* 41	0	1
	* 57	0	1
	U* 63	0	1
6	* 6	0	1
	U 19	0	1
	U 20	1	0
	U* 48	1	0
7	24	0	1
	29	0	1
	U* 30	0	1
	U* 31	0	1
	33	0	1
	U 36	2	1
	U 38	1	2
	* 39	1	2
	47	0	1
	†division of mental scale (E. E. Williams, pers. comm.).		
8	U* 34	0	3
	39	0	1
	41	0	1
	U* 46	0	1
	* 56	0	1
9	U* 45	1	0
	50	0	1
10	* 13	0	1
	14	0	1
	U* 21	0	1
	U 27	1	0
	U 36	1	2
	* 51	0	1
	52	0	1
	U 61	0	2

Appendix 2 continued.

STEM	TRANSFORMATION SERIES	ANCESTRAL CHARACTER	DERIVED CHARACTER
11	7	0	1
	U 40	0	1
12	8	0	1
	10	2	3
	41	0	1
	†sharp canthal ridge acquired (Etheridge and de Queiroz, 1988; Lang, 1989).		
13	* 9	0	1
	10	0	2
	11	0	1
	U 34	0	2
	U 63	0	1
14	U* 21	1	0
15	U 59	0	1
	66	0	1
	†dorsal scales enlarged relative to laterals (Larsen and Tanner, 1975).		
16	U 35	0	1
	42	0	1
17	5	0	1
	9	0	1
	†scleral ossicle 6 reduced or lost (de Queiroz, 1982).		
	†row of enlarged chinshields that increase in size posteriorly (Montanucci *in* Etheridge and de Queiroz, 1988).		
	†anterior fibers of *m. retractor lateralis anterior* reflected outwards or posteriorly before insertion (Arnold, 1984).		
18	28	0	1
	U 30	0	1
	33	0	1
	53	0	1
	U 59	1	0
	U 60	0	1
	U 62	0	1
	†scleral ossicle 8 reduced (de Queiroz, 1982).		
19	33	0	1
	42	0	1
	U 61	1	2
	U 64	0	1
20	* 1	1	0
	U* 18	0	1
	* 24	1	2
	U 36	1	0
	55	0	1
	U 61	0	1
21	U 20	0	1
	U 21	1	2
	U 46	1	0
	U 59	1	0
22	12	0	2
23	U* 17	1	0
	24	1	0
	U 35	0	1
	49	0	1
	54	0	1

Appendix 2 continued.

STEM	TRANSFORMATION SERIES	ANCESTRAL CHARACTER	DERIVED CHARACTER
24	* 1	0	1
	U* 18	1	0
	U 23	0	1
	47	0	1
25	12	0	1
	* 24	1	2
	U 37	1	0
	U 40	0	2
	43	0	1
	52	0	1
	U 58	0	1
26	U* 17	0	1
	U 22	0	1
	U 48	0	1
27	U* 37	0	1
	39	0	1
	U 44	1	0
	U 45	1	0
	* 54	1	0
28	9	0	1
	U 21	1	0
	U 27	1	0
	U 36	1	0
	U 38	1	0
	†females acquire gravid coloration (Medica *et al*, 1973) (also in some phrynosomatids [e.g., *Holbrookia* (Axtell and Wasserman, 1953), *Petrosaurus mearnsi*] and some tropidurids [e.g., *Tropidurus thoracicus* (Dixon and Wright, 1975)]).		
29	U 20	1	0
	24	0	1
	U 46	0	1
30	12	0	1
	U 18	1	0
	25	0	1
	U 34	0	1
	U 38	1	2
	U 59	1	0
	65	0	1
31	U 35	1	0
	U 48	1	0
	* 54	0	1
32	†frontals fused embryonically (Jollie, 1960).		
	†frontals constricted between the orbits (Estes *et al.*, 1988) (modified in some taxa).		
	†broad frontal shelf underlying nasals (Estes *et al.*, 1988).		
	†postfrontal reduced (Estes *et al.*, 1988; Presch, 1988).		
	†parietal foramen on frontoparietal suture (Estes *et al.*, 1988) (modified in some taxa).		
	†iguanian brain morphology (Northcutt, 1978).		
	†*m. intercostalis ventralis* lost (Camp, 1923).		
	†tongue mucocytes mostly serous and sero-mucous (Gabe and Saint-Girons, 1969; Schwenk, 1988).		

APPENDIX 3

Lists of changes within transformation series for tree in Figure 9. See legend of Appendix 1 for abbreviations used. Asterisks note character shifts that are of ambiguous placement. Characters from unpolarized or unordered transformations are noted by a "U."

Transformation Series	Changed From	To	Along Stem	Consistency
1	* 0	1	24	
	* 1	0	20	0.500
2	0	1	5	1.000
3	* 0	1	5	
	* 1	0	2	0.500
4	0	1	2	1.000
5	0	1	17	
	0	1	POLYC	
	0	1	UROMA	0.333
6	* 0	1	6	
	* 1	0	2	
	* 1	0	PRISC	0.333
7	0	1	11	
	1	0	3	
	0	1	CROTA	
	0	1	LAEMA	0.250
8	* 0	1	4	
	0	1	12	
	0	1	PHRYN	0.333
9	0	1	5	
	0	1	28	
	0	1	17	
	* 0	1	13	
	0	1	CHALA	
	* 1	0	LAEMA	0.167
10	0	2	13	
	2	3	12	
	0	1	IGUAN	
	0	1	LEIOC	0.600
11	0	1	13	
	0	1	DIPSO	0.500
12	0	1	30	
	0	1	25	
	0	2	22	0.667
13	* 0	1	10	
	0	1	CORYT	
	* 1	0	PRIST	0.333
14	0	1	10	1.000
15	0	1	1	1.000
U16	0	1	4	1.000
U17	* 0	1	26	
	0	1	4	
	* 1	0	23	
	0	1	LIOLA	
	0	1	ANOLE	
	0	1	ENYAL	0.167

Appendix 3 continued.

Transformation Series	Changed From	To	Along Stem	Consistency
U18	* 1	0	24	
	1	0	30	
	* 0	1	20	
	1	0	ENYLD	
	1	0	ANOLE	0.200
U19	0	1	6	1.000
U20	1	0	29	
	1	0	6	
	0	1	21	0.333
U21	* 1	0	14	
	* 0	1	11	
	* 0	1	4	
	* 1	0	28	
	1	2	21	
	1	0	PHYMA	
	* 0	1	CORYT	
	1	2	ANOLE	0.250
U22	0	1	26	
	0	1	ANOLE	0.500
U23	0	1	24	
	1	0	STENO	
	0	1	ANOLE	0.333
24	0	1	29	
	* 1	2	25	
	1	2	20	
	1	0	23	
	0	1	7	
	1	2	ANOLE	0.333
25	0	1	30	
	0	1	ENYLD	0.500
26	0	1	5	1.000
U27	1	0	10	
	1	0	28	
	0	1	POLYC	0.333
28	0	1	18	
	0	1	4	0.500
29	* 0	1	7	1.000
U30	0	1	18	
	* 0	1	5	
	* 0	1	7	
	0	1	CHALA	
	0	1	PHYMA	
	* 1	0	PHYSI	0.167
U31	* 0	1	7	
	0	1	1	
	0	1	CORYT	0.333
U32	0	1	LEIOC	
	0	1	UROMA	
	0	1	AGAMI	0.333
33	0	1	18	
	0	1	19	
	0	1	7	0.333
U34	0	1	30	
	0	2	13	
	0	3	8	1.000

Appendix 3 continued.

Transformation Series	Changed		Along Stem	Consistency
	From	To		
U35	1	0	31	
	0	1	23	
	0	1	16	
	1	0	SCELO	0.250
U36	1	2	10	
	1	0	28	
	1	0	20	
	2	1	7	
	1	0	IGUAN	
	1	0	LIOLA	
	1	0	UROMA	0.286
U37	0	1	27	
	0	2	3	
	1	0	25	0.667
U38	* 1	2	5	
	1	2	30	
	1	0	28	
	1	2	7	
	1	2	OPLUR	
	1	0	PHYMA	
	1	0	PETRO	0.286
39	0	1	27	
	* 0	1	5	
	0	1	8	
	1	2	7	
	* 1	0	2	
	1	0	OPLUR	
	1	0	PHYMA	
	1	0	PETRO	
	1	2	CHAME	0.222
U40	0	1	11	
	1	0	3	
	0	2	25	
	0	1	BRACH	0.500
41	* 0	1	5	
	0	1	12	
	0	1	8	
	0	1	BRACH	
	0	1	CROTA	0.200
42	0	1	19	
	0	1	16	0.500
43	0	1	25	1.000
U44	1	0	27	
	1	0	DIPSO	
	0	1	URANO	
	1	0	BASIL	0.250
U45	1	0	27	
	* 1	0	9	
	1	0	DIPSO	
	0	1	URANO	
	0	1	CTENO	
	1	0	BASIL	0.167

Appendix 3 continued.

Transformation Series	Changed From	To	Along Stem	Consistency
U46	0	1	29	
	1	0	21	
	* 0	1	8	
	0	1	2	
	1	0	CHALA	0.200
47	0	1	24	
	0	1	7	
	1	0	URANO	
	0	1	SCELO	
	0	1	CHAME	0.200
U48	1	0	31	
	0	1	26	
	* 1	0	6	
	* 1	0	POLYC	
	0	1	CHAME	0.200
49	0	1	23	1.000
50	0	1	9	1.000
51	* 0	1	10	
	* 1	0	POLYC	0.500
52	0	1	10	
	0	1	25	
	1	0	POLYC	0.333
53	0	1	18	1.000
54	* 0	1	31	
	* 1	0	27	
	0	1	23	0.333
55	0	1	20	1.000
56	* 0	1	8	1.000
57	* 0	1	5	
	1	0	PHYSI	0.500
U58	0	1	25	
	0	1	CHAME	0.500
U59	1	0	18	
	1	0	30	
	1	0	21	
	0	1	15	
	0	1	URANO	0.200
U60	0	1	18	1.000
U61	0	2	10	
	0	1	20	
	1	2	19	0.500
U62	0	1	18	
	0	1	LEIOL	0.500
U63	* 0	1	5	
	0	1	13	0.500
U64	0	1	19	
	0	1	ENYAL	0.500
65	0	1	30	
	0	1	UROMA	0.500
66	0	1	15	
	0	1	SANDL	0.500
67	* 0	1	4	
	0	1	ANOL	0.500